MedWet

Conservation of Mediterranean Wetlands

Vegetation of temporary marshes

Ecology and management

P. Grillas & J. Roché

The Tour du Valat would like to thank the Conservatoire botanique national de Porquerolles,
Joël Mathez (Montpellier University), Dianne Wilker
and all those who have been involved in the production of this publication.

Production : Tour du Valat
Design : Tapages Publics
Cover : Sonia Viterbi
Illustrations : Sonia Viterbi
Translated from French by Alison Duncan

Prepared and published with the financial support of the European Community.

ISSN : 1271-8831 ISBN : 2-910368-16-5
(ISBN : 2-910368-15-7 - Edition française)

Tour du Valat
Le Sambuc - 13200 Arles - France
Fax : ++ 33 (0)4 90 97 20 19
E. mail : secretariat@sansouire-tourduvalat.fr

Printed in France
at the Imprimerie De Rudder, Avignon

on chlorine-free paper

MedWet

The MedWet action

The Mediterranean basin is rich in wetlands of great ecological, social and economic value. Yet these important natural assets have been considerably degraded or destroyed, mainly during the 20th Century. To stop and reverse this loss, and to ensure the wise use of wetlands throughout the Mediterranean, a concerted long-term collaborative action has been initiated under the name of MedWet.

A three-year preparatory project was launched in late 1992 by the European Commission, the Ramsar Convention on Wetlands of International Importance, the governments of Spain, France, Greece, Italy and Portugal, the World Wide Fund for Nature, Wetlands International and the Station Biologique de la Tour du Valat.

This project focuses on that part of the Mediterranean included within the European Union, with pilot activities in other countries such as Morocco and Tunisia. Two-thirds of the funds are provided by the European Union under the ACNAT programme and the remainder by the other partners.

The concept of MedWet and its importance for the wise use of Mediterranean wetlands was unanimously endorsed by the Kushiro Conference of the Contracting Parties to the Ramsar Convention in June 1993.

The MedWet publication series

Wetlands are complex ecosystems which increasingly require to be managed in order to maintain their wide range of functions and values. The central aim of the MedWet publication series is to improve the understanding of Mediterranean wetlands and to make sound scientific and technical information available to those involved in their management.

Patrick Grillas & Jean Roché, 1997
Vegetation of temporary marshes, ecology and management
Conservation of Mediterranean Wetlands - number 8
Tour du Valat, Arles (France), 86 p.

Titles of the collection:

1. Characteristics of Mediterranean Wetlands
2. Functions and Values of Mediterranean Wetlands
3. Aquaculture in Lagoon and Marine Environments
4. Management of nest sites for Colonial Waterbirds
5. Wetlands and Water resources
6. Aquatic emergent Vegetation, Ecology and Management
7. Conservation of Freshwater Fish
8. Vegetation of temporary Marshes, Ecology and Management

Conservation of Mediterranean Wetlands
MedWet

Vegetation of temporary marshes

Ecology and Management

P. Grillas and J. Roché

Number 8

Series editors : J. Skinner and A. J. Crivelli

J. Roché

Preface

The Medwet programme is recognised globally as a unique and innovative initiative and the MedWet publication series is becoming a key reference for Mediterranean wetland managers, as well as for decision-makers involved in defining policies for biodiversity conservation.

The series deals in turn with all the major elements determinant for the complex task of conserving Mediterranean wetlands. From the description of their ecological characteristics to the conflicts of interest between different resource users, the analysis is detailed, well-explained and easy to understand.

In addition, this series has a twin objective. On the one hand it promotes an integrated approach to the scientific understanding of wetlands and to resolving the long term conservation issues facing managers and decision-makers. On the other, it promotes a regional perspective which underlines both the similarities and the differences within the Mediterranean region.

Mediterranean temporary marshes are a unique habitat. It is the irregular seasonal fluctuations in the water cycle that make these wetlands not only a dynamic habitat of scientific interest, but also extremely fragile in the face of anthropogenic pressure which rapidly affects their species composition.

A better understanding of the vegetation of these marshes, their natural trends and their response to annual environmental fluctuations therefore exceeds the narrow interest of erudite academics. This volume provides managers with a first-rate tool which will allow them to detect habitat degradation, and gives decisions-makers the means to implement the measures required to correct, or avoid, the pernicious effects of erroneous policies.

Juan Manuel de Benito
Director of the European Topic Centre of Nature Conservation
European Environment Agency

***Damasonium stellatum*, one of the many rare or threatened species of temporary marshes.**

Contents

J. Roché

Introduction

Wetlands are situated on the interface between terrestrial and aquatic habitats. This intermediate position within the landscape, and the diversity of types of wetlands makes it difficult to define them precisely.

It is even more difficult to provide a definition of temporary marshes. During the submerged phase temporary marshes are clearly wetlands, whereas during the dry phase they do not look like wetlands at all and may even appear arid. Despite the transitory nature of the flooding, which sometimes only lasts a few weeks, the ecological importance of the aquatic phase is so great that temporary marshes must be classified as wetlands.

Temporary marshes occupy depressions, often endorheic*, which are flooded for a sufficiently long period to allow the development of aquatic vegetation or hydromorphic* soils. The water supply comes either directly from rain, or indirectly from the watershed (run-off) and from the water table. Marshes in direct physical contact with habitats subject to permanent flooding (lake edges, permanent marshes) are not included in this definition of temporary marshes. This very general definition is

Temporary marshes are typical habitats of Mediterranean deltas. Cerisières, Camargue, France.

** Refer to glossary, page 80*

based on their essential ecological characteristics, i.e. the alternation of flooded and exposed periods with hydrological isolation, at least for the surface water. Widely distributed over the world, temporary marshes occur under a multitude of climatic conditions, for example Arctic, temperate, tropical or desert. They are typically Mediterranean, but also occur in similar climates around the world (Australia, California, South Africa). They are found from the mountains to the sea, and sometimes, in the case of certain endorheic basins, below sea level.

The fauna and flora of temporary marshes are perfectly adapted to living in habitats with unpredictable flooding.

The great temporal variation of conditions (especially hydrological) is the most remarkable ecological characteristic of temporary marshes. Some experience an increase in water salinity from a few g/l to more than 100 g/l within a period of a few weeks (on the coast, in deltas, and endorheic basins) or have a sharp reduction in the area of surface water. The duration and frequency of flooding are extremely variable from one year to the next, and from one marsh to another. In the Mediterranean region, many dry out each year (seasonal marshes); in more arid climates they can remain dry for several years (non-seasonal). The ephemeral marshes are briefly flooded each year, or less frequently. Semi-permanent marshes dry out only in certain years or very briefly each year. Thus there exists a huge variety of temporary marshes whose hydrological and biological characteristics depend on the substrate, the geomorphology and, in large part, the climate.

In the Mediterranean climate, the rain which falls between autumn and spring is the source of water. The wet period occurs when temperatures are relatively low, and the marshes dry out quickly in the hot, dry summers. The temporary nature of these marshes thus results from a combination of low precipitation and high evaporation which leads to a characteristic summer water deficit.

The size of Mediterranean temporary marshes varies considerably, from the immense sebkhas of several thousand hectares (North Africa), large coastal marshes (Marismas del Guadalquivir, Spain), isolated marshes of a few ares or hectares, to the rock pools of a few tens of metres square on rocky substrates (Provence, France, Sicily). In general, their distribution around the Mediterranean basin and their fragmentation within the different regions means that they are a relatively isolated habitat.

This does not detract from their ecological importance, particularly with respect to vegetation. The extreme and unstable environmental variations in the temporary marshes subjects the flora to conditions ranging from aquatic to arid. In response, they have developed remarkable survival strategies, including adaptations in size, form, reproduction and life cycle. The fauna, also, has adapted to the same constraints and these habitats therefore support genetic resources which are not only diverse, but of great value. There are numerous rare species and many have unusual ways of life. The plant communities, which are dominated by herbaceous species, are organised to deal with the alternation of flooding and drying out. Aquatic vegetation is dominant during the flooded period, amphibious vegetation during the transitional period, and terrestrial plants during the dry summer period. This pattern occurs differently in different places and varies with the seasons and between years.


L. Tan Ham

***Juncus striatus*, a typically delicate marsh plant.**

Paradoxically, temporary marshes, ideal laboratories for studies of the living world, are little known in terms of their vegetation and fauna. This is particularly regrettable as they are now rare and in danger of disappearing. Modern agriculture allows these generally flat habitats, with small volumes of water, to be drained to provide fertile farmland. Industry and tourism, great consumers of space, also completely transform these marshes. A more unusual threat for these wetlands is the development of near-permanent bodies of water under the auspices of flood regulation projects, or management for hunting, fish-farming or wildlife conservation. Management of these "forgotten" habitats, helped by powerful modern equipment and finance, is destroying temporary wetlands before we have a clear vision of their importance.

The aim of this brochure is to contribute to the conservation of Mediterranean temporary wetlands through recognition of their richness and the characteristics of their ecological functioning. This review is based on the available knowledge of their vegetation and general ecology and has been compiled in the hope of providing the key to their conservation, management and restoration.

J. Roché

The diversity of temporary marshes

Temporary marshes occur throughout the Mediterranean basin. They occupy depressions where water accumulates for periods varying from a few days to several months.

Temporary marshes include a great diversity of habitats which can be distinguished by their size, climatic region, substrate and topography. They are classified according to the annual drying-out period which constitutes the dominant ecological constraint in all situations.

Some marshes flower colourfully in the spring. Acheloos, Greece.

Diversity of habitat: a few examples

A large deltaic marsh in Spain

The marismas of the Guadalquivir delta cover 27,000 ha of temporary seasonal marshes protected by the National Park of Doñana. This vast fluvial-marine clay basin floods regularly with rainwater from the Rocina stream and the Guadalquivir river. From October to March, the area is flooded with 20-40 cm water. From March to June, the marsh gradually empties, and is dry between July and September. The marismas include a wide range of temporary marshes, saline, brackish, and freshwater, either in small basins or over huge areas of uniform depth, on sandy substrate between the dunes, or on silt.

The many faces of the Algerian sebkhas

Sebkhas are very flat depressions, often less than a metre deep, on a silty and/or sandy substrate, extending from several tens of hectares to several tens of km^2. They occur in coastal plains (Oran region) and at altitude (800 m on the Constantine plateau) in a cultivated or steppe environment. They are fed by rainwater and run-off, but have very high evaporation, several times higher than the quantity of rainfall and dry out each year for several months. The length of the dry period varies between years, and between the west and east of Algeria. In the more arid west of the country, the dry period is long and the very high salinity often prevents the development of aquatic vegetation. In the east the climate is wetter, so the flooded period is longer and can, exceptionally, last as long as two years.

P. Grillas

The celebrated marshes of Doñana, Spain, support large populations of wintering waterfowl.

The diversity of temporary marshes

Even small ponds may harbour 15-20 species of submerged plants. Roquehaute, France

L. Tan Ham

Artificial seasonal pools in the Languedoc, France

In the south of France, at Roquehaute, small pools are found on ancient basaltic flows from one of the most southern volcanoes of the Puy chain. They have been formed by quarrying the rock for building material. Each year these ponds on impermeable soil are filled with rainwater. Their depth varies from a few centimetres to 1 metre and their area is a few tenths of a hectare. The length of the drying out period is very variable, and depends on the size of the pool and its morphology. The deepest pools can sometimes retain a little water even in the middle of summer. Covering less than 200 ha, and each separated by a few tens of metres, this chain of 200 pools is isolated in the middle of the maquis and the garrigue.

Diversity of habitats, diversity of names

Many different names are given to temporary marshes, and they vary a great deal from one region to another, reflecting the diversity of forms of these ecosystems. In France the "lavognes" of the Causses region, the "laquets" of the Nimes region, and the "baisses" of the Camargue, are different types of marshes, but they are all temporary. In North Africa, too, several terms are used for these habitats: "daya", "sebkha" or "chott".

Habitats with multiple constraints

Plants have three basic requirements: light, water and nutrients. They also need oxygen for respiration. Access to these resources is completely different during the wet and dry periods in the life of a marsh.

Light energy

All autotrophic* plants are dependent on light as the energy source for photosynthesis, and most food chains begin with these plants. Penetration by light is therefore essential in these ecosystems. Light penetrates water with difficulty for several reasons, among which the most important are:

- From 2-100 % of the sun's rays[1] are reflected back from the water surface: this "mirror" effect of water bodies increases when the sun is low.
- The particles (or the organisms) in suspension also reflect light.
- Water, suspended particles, solutes and planctonic life all absorb light energy in the form of heat.

So the available light decreases rapidly with depth and the rate of attenuation depends on the characteristics of the water. The available light for the submerged plants is also reduced by trees along the banks, and communities of helophytes* (e.g. *Phragmites, Typha, Scirpus*).

Emergent plants, and to an even greater degree, terrestrial plants, can obtain light energy more easily than submerged plants.

Nutrient resources

Terrestrial plants obtain their nutrients from the air (carbon) and the soil, whereas submerged plants extract them from water and the soil. Access to nutrients is often more difficult for submerged plants than for terrestrial ones. The nutrients are less abundant in water than in the soil, and in wet conditions, because of the lack of oxygen, they are present in the soil in a chemical form that is not accessible to the plants. The absence of oxygen in the sediment encourages the formation of compounds which are toxic to plants (e.g. Fe^{++},S^{--}).

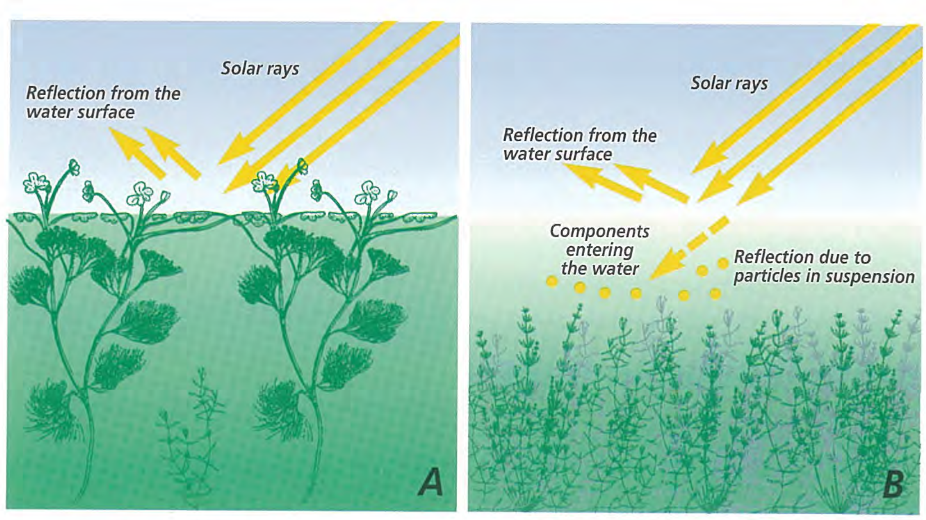
Inorganic carbon is essential for photosynthesis and terrestrial plants take it from the air where it is abundantly available in the form of carbon dioxide. In water CO_2 is much less abundant than in the air; its solubility decreases as the temperature increases, and the speed of diffusion is slow, particularly in stagnant water.
Inorganic carbon exists in water in different forms, the concentrations of

1 - Kirk 1986

which vary with the pH: carbon dioxide (CO_2), carbonate (HCO_2^-) and bicarbonate (CO_3^{--}). When the pH is slightly higher than neutral, the water is rich in carbonates. In some soils, such as siliceous sand or non-calcareous soils (pH<5), the water is low in carbonates and only CO_2 is present in any significant quantity.

Certain aquatic plants have developed the capacity to use the carbonates (HCO_3) as their source of inorganic carbon[1], which is not known to occur in terrestrial species. The presence of high concentrations of carbonates associated with calcium is not tolerated by some species.

In temporary marshes the alternation of wet and dry periods favours mineralisation and the recycling of organic matter. During the flooded periods significant denitrification* occurs, leading to a loss of nitrogen from the sediment by its transformation into the gas N_2, which escapes into the atmosphere. Nitrogen is therefore often the limiting element for plant production in marshes, whereas phosphate is usually limiting in deep lakes. Excessive amounts of phosphate and nitrogen, which often result from pollution due to agriculture or domestic waste, lead to eutrophication* of wetlands. In temporary marshes this is characterised by a decline in the floristic richness, either by the replacement of the less productive species by helophytes, or by the development of filamentous algae.



Species which develop floating leaves prevent light from reaching the plants below (A). When no floating leaves are present, light is reflected at the surface, and water must be shallow for the plants to grow (B).

1 - For example: Keeley & Sandquist, 1992

The toxicity of the ions, and the necessary expenditure of energy by the plants to counteract the effects of the salts, can seriously affect the growth and development of certain species. Other elements such as calcium can also influence the presence or the abundance of some plants.

Toxic ions

Nutrients are not the only elements to dissolve in water. Other ions, present sometimes in large quantities, can affect the species composition of the plant communities and the growth of the plants. Salinity (generally due to the ions Na^+, Cl^-, SO_4^{--}) stresses both terrestrial and aquatic plants. Present in the sediment and/or the underground water table, the salts rise to the surface by capillary action drawn up by the strong evaporation in the summer. This evaporation can lead to a layer of salt forming on the soil surface, which has a double effect on the plants. By raising the osmotic pressure*, it limits access to the water and the dissolved nutrients (and could be considered a physiological drought). The toxic ions, easily assimilated, reduce the efficiency of the enzymatic and metabolic processes, particularly the synthesis of proteins.

Oxygen

The availability of oxygen, vital for respiration, divides the aquatic from terrestrial habitats. Terrestrial plants benefit from a non-limiting source of oxygen in the atmosphere. In water, the solubility of oxygen is low and decreases with increasing temperature. The oxygen content of water depends on the supply from daily photosynthesis, its consumption by plants and animals for respiration, and by micro-organisms which decompose the organic matter in the sediment. The oxygen requirement is higher for the underground organs due to the oxygen consumption in the soil for the mineralisation of organic matter. Different terrestrial and amphibious plant species have very different tolerances of asphyxiation in water-saturated soils[1].

1 - Crawford, 1989

The diversity of temporary marshes

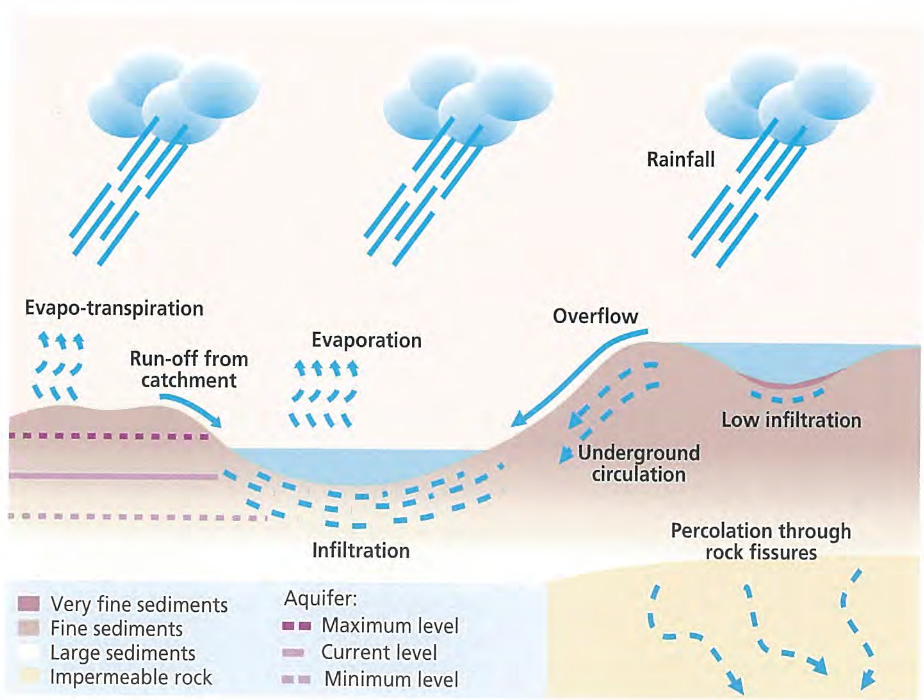
The water supply

In Mediterranean temporary marshes, terrestrial plants are exposed successively to too much and too little water. For aquatic plants, drought is the principal threat; flooding is the dominant constraint for the terrestrial species.

Little supply and great losses

The supply of water to temporary marshes comes directly from rain, surface run-off, or from groundwater. In a given situation one or the other source of water usually dominates. Direct rainfall is often the principal source of water for temporary marshes. In the Mediterranean climate, it falls in autumn and/or spring, depending on the region. The water supply of wetlands on the plains, or temporary lakes in karstic* regions (e.g. Croatia), is heavily influenced by the underground water table. In marshes with an impermeable bottom, the run-off, and therefore the watershed, becomes more important.

Water loss from marshes occurs in several ways, principally by evapo-transpiration, infiltration, percolation, and outflow. In the Mediterranean climate direct evaporation of the water and transpiration by plants are very strong in the summer, and their impact is increased by wind. Losses by vertical percolation are dependent on the permeability of the substrate. In compact rocks (calcareous, granitic, basaltic, etc.) percolation can only occur through cracks or fissures. In permeable soils (clayey or sandy) water infiltrates through the entire area of the bottom of the marsh. The granulometry of the sediment



Water levels in temporary marshes are determined by the interaction of run-off, evaporation and infiltration.

controls the quantity of water which is lost: the speed of infiltration increases with the size of the particles and the way they are positioned (texture and structure). Even on a coarse substrate, the fine sediments in the marsh can create a layer of impermeable clay which limits or stops infiltration.

The flooding period results from an excess of supply over loss. This usually occurs between autumn and the end of winter, due to heavy rains and a low evapo-transpiration rate. Conversely, in the spring the losses increase quickly as the temperature rises.

A highly variable water balance

The supply of water to the marshes is subject to a great deal of variability, in time and in space.

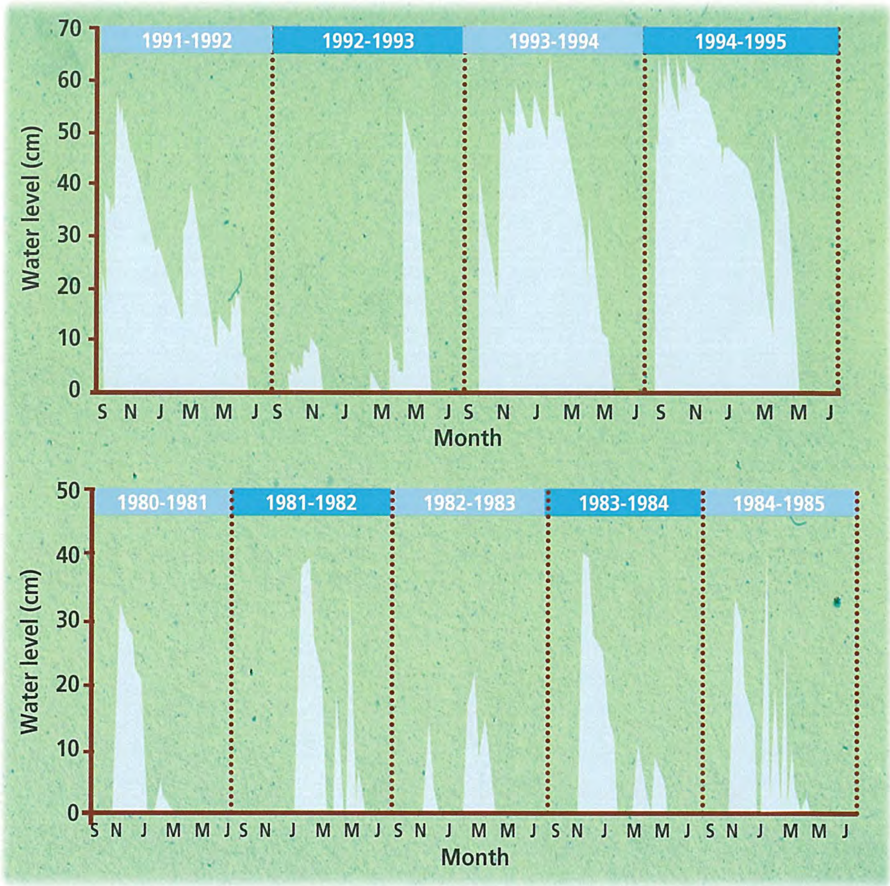
For the flora and fauna, three hydrological parameters of temporary marshes are particularly important: the date of flooding, its duration and the depth of water. These values are extremely variable from one site to another depending on local conditions and the relative size of the inputs and outputs of water. The topography, particularly the relation of volume to surface, affects the water retention capacity.

There is also an annual variation in the water level. On a given site, the date, depth and duration of flooding can fluctuate considerably according to the annual rainfall.

Substrate	Hydraulic conductivity (m/day)
Gravel	*150 - 450*
Dune sand	*20*
Sand	*2.5 - 45*
Granite (weathered)	*1.4*
Limestone	*0.94*
Sand stone	*0.2 - 3.1*
Schist	*0.2*
Silt	*0.08*
Basalt	*0.01*
Dolomite	*0.001*
Clay	*0.0002*
Slate	*0.00008*

The hydraulic conductivity of selected substrates. After Todd, 1980.

The diversity of temporary marshes



Variations in water levels in four consecutive years in two temporary marshes: Above: La Cerisière sud, in Camargue, France. Below: Marrakech in Morocco After Dupuis, 1988.

The Moroccan dayas

The dayas in the Marrakech region are small (several hundreds of m^2), round, and very flat (less than 30 cm in depth). They are formed by the action of water and wind. In this region whirlwinds of hot air often start in the same place. They carry dust and sand which gradually wear away shallow depressions which collect rainwater. During the wet period, October to February, the underlying schist base rock is broken down into fine particles of clay and silt which are carried off during the next dry period. In this way the daya is gradually formed.

However, the finest particles of clay tend to be deposited, year after year, to form a compact sediment capable of resisting the wind erosion. The erosion is stabilised in the centre but may continue to extend the edges of the daya.

After Boutin *et al.*, 1982

J. Roché

Vegetation and fauna of temporary marshes

Temporary marshes have three distinct phases to their annual cycle: wet (flooded phase), humid (drying out phase) and terrestrial (dry phase).

The variability of the ecological conditions allow many different animal and plant species to use this habitat. The instability, however, is a strong limitation. Few living creatures can survive these contrasts all year round, so different species try to escape the stress of the periods which are unfavourable to them. Resistant forms (seeds of plants, eggs of invertebrates) with reduced activity enable some plants and animals to avoid inhospitable conditions. Other species, principally animals, leave the marsh when the conditions are no longer favourable to them (e.g. amphibians and airborne adults whose larvae are aquatic, such as dragonflies).

Temporary marshes play host to many insects with aquatic larvae. ***Ischnura elegans.***

The plant communities

On a single site the succession of contrasting ecological conditions (from aquatic to terrestrial, or from freshwater to saline) offer an ecological niche to a multitude of species (aquatic, amphibious, terrestrial, more or less halophytic*, etc.) ; the flora is therefore rich in comparison with surrounding habitats.

From one site to another, hydrological conditions, substrate, salinity and climate differ greatly, so the plant communities are also very different, and include a large number of species.

The diversity of plant communities is more difficult to evaluate than species diversity. One approach is the classification of plant associations over the whole of Europe (CORINE system). This system groups formations which are similar in terms of their floristic composition as well as the predominant ecological conditions.

In simple terms, two main categories of plant communities can be distinguished as a function of water salinity.

Botanical richness of pools in Provence, France

The floristic richness of temporary marshes in Provence (the Massifs of Estérel and the Maures, in the Crau) depends mainly on their size. The largest (several hectares), hold 60-100 species. The smallest (erosion dips in the rock, tens of square metres) only contain 15-20. The largest of these marshes, situated on calcareous rock in the Crau, is also the richest, containing 104 species. Many species are very sparsely represented: 40-50 % are present in fewer than one in ten plots. In contrast the species in permanent marshes are limited to a dozen abundant species, such as *Phragmites, Scirpus, Potamogeton, Nuphar.*

After Barbéro *et al.*, 1982

Vegetation and fauna of temporary marshes

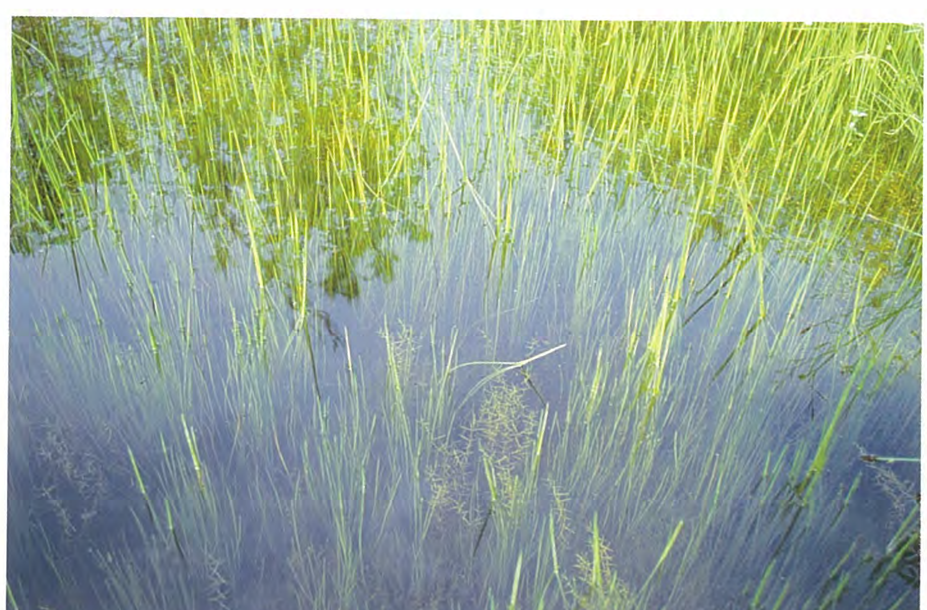
The plant associations of freshwater marshes

Freshwater marsh flora is principally dependent on water depth and carbonate levels.

- In small, shallow marshes on non-calcareous substrates, often with acid water, the following plant associations dominate: Isoetes (*Isoetes durieui, I. velata, I. hystrix,* etc.) and rushes (*Juncus bufonius, J. pygmaeus, J. capitatus,* etc.). A number of these species are rare and protected on a regional, national or European level. Several families of ferns are also represented *(Isoetaceae, Marsileaceae).*

- In marshes on calcareous substrates the water is richer in nutrients, and minerals, and is occupied by a rich community of long-leafed aquatic plants: *Myriophyllum* family *(M. alterniflorum), Zannichellia* family *(Z. pedunculata and Z. obtusifolia), Chara* family *(C. aspera and C. vulgaris),* and certain pondweeds *(Potamogeton pusillus, P. trichoïdes).* The *Callitriche* family sometimes dominate *(C. truncata, C. brutia)* as well as white flower *Ranunculus* (sub-genus *Batrachium*) such as *R. peltatus* or *R. aquatilis* etc. Some species of *Characeae* are also present, e.g. *Chara aspera, C. vulgaris* and *Tolypella glomerata.*

- Some marshes are almost entirely populated by *Characeae,* of the genus *Chara* on calcareous substrates, and *Nitella* on non-calcareous substrates.



P. Grillas

Isoetes setacea **– a rare species related to ferns.**

The plant associations of brackish and salt marshes

These marshes fall into two main types:

- Marshes whose vegetation is composed of non-vascular plants (*Characeae* of the genus *Lamprothamnium, Tolypella, Chara spp.*).

- Marshes whose vegetation is comprised of vascular plants (*Ruppia, Ranunculus, Zannichellia,* etc.). The botanical composition varies according to conditions (depth, water salinity, length of flooding, grazing regime). The helophytes (*Scirpus sp., Eleocharis sp., Typha sp.*) may dominate in these habitats[1] and certain terrestrial species (*Aeluropus littoralis, Suaeda maritima, S. splendens, Limonium spp., Cressa cretica,* etc.) can benefit from the drying out period to cover large areas.

Characeae, remarkable plants

The *Characeae* are abundant in many temporary marshes. Although their form resembles that of flowering plants, they are in fact green algae intermediate in form between primitive algae and mosses, the oldest species of which appeared about 400 million years ago. The family *Characeae* has only six genera: *Chara* is the commonest and most diverse genus in the Mediterranean (twenty species). The *Characeae* produce female gametes* protected by a hard shell (oogonia), foreshadowing reproduction by seeds which developed much later in higher plants. These algae possess a remarkable aptitude for assimilating calcium, to the point that *Chara* consists of almost 70 % calcium carbonate[2]. Their fast growth can modify the physicochemical characteristics of water, as suspended particles become trapped between their strands, thus reducing the calcium concentration and the turbidity. The abundant stands of *Chara* create a habitat for many animals (a place to lay eggs, and feeding grounds for fish and insects) and at the same time they provide a food source for gastropods, carp and ducks[3].

1 - See n° 6 in the MedWet series
2 - El Khiati, 1987
3 - Guerlesquin & Podlejski, 1980

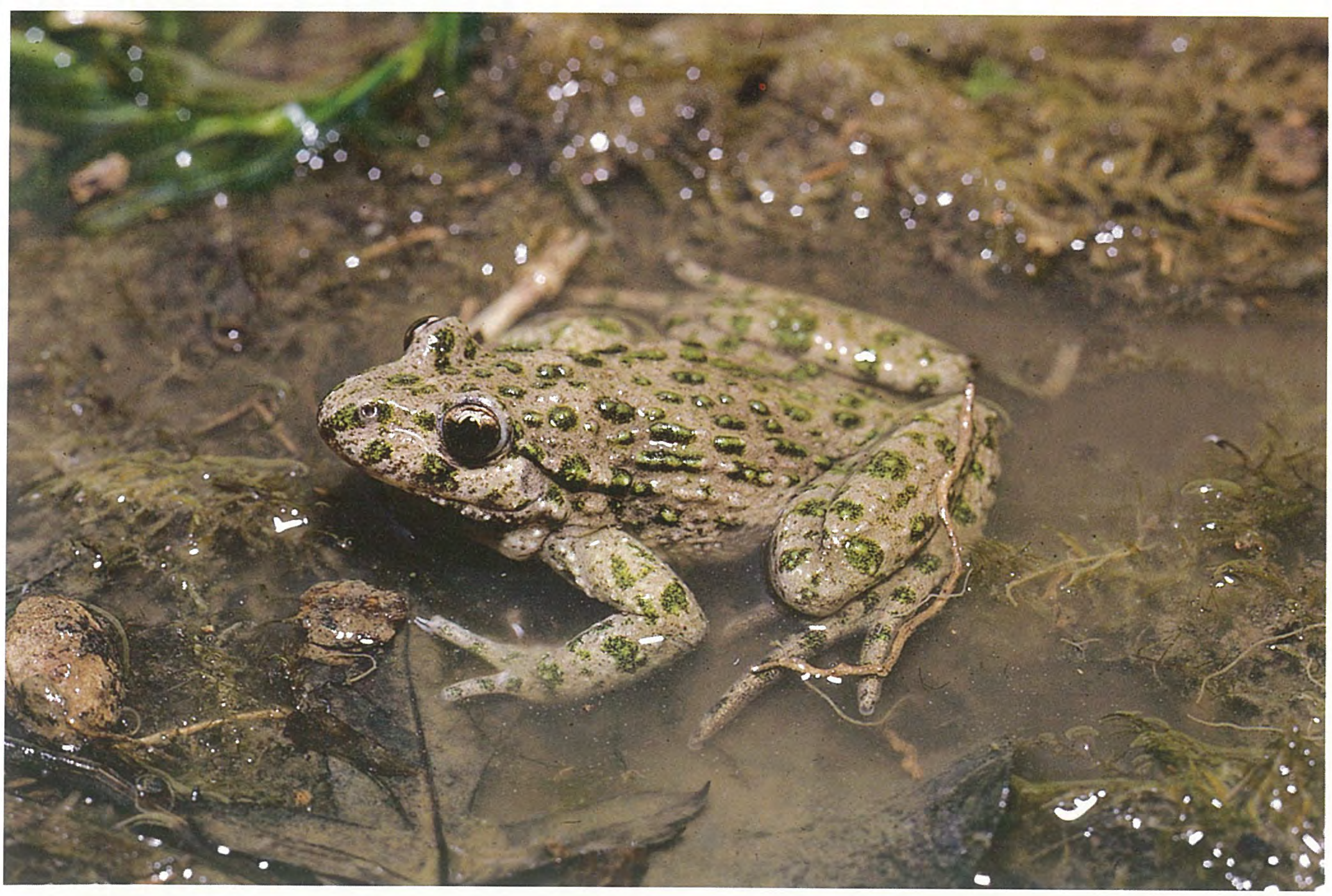
The fauna

The fauna of temporary marshes is made up of species which are dependent on aquatic habitats to very different degrees.

Some of them are characteristic of temporary habitats, while other more widespread species are as abundant in permanent aquatic habitats. The most characteristic species of temporary marshes have a life cycle with two main phases, aquatic and terrestrial, e.g. the amphibians, and many species of invertebrates (such as dragonflies and mosquitoes).

The species which use temporary marshes only for feeding are generally widespread and do not depend solely on this habitat, moving on when the marsh dries out.

The Parsley frog, *Pelodytes punctatus* lays its eggs in February so the tadpoles can metamorphose before the marsh dries out.



J. C. Malausa / Bios

J. Roché

Triops survive the dry season as eggs.

Invertebrates

They constitute a large and diversified group. Many of the species are ubiquitous, but the communities differ from those in permanent marshes. The copepods, phyllopods and ostracods are characterised by their more or less constant presence[1]. In contrast, the isopods, amphipods and decapods are often absent, or less abundant.

Fish

Strictly aquatic, fish cannot colonise temporary marshes if they are not in periodic connection with permanent aquatic habitats. If fish do manage to get into the temporary marsh, they can breed, but success is not guaranteed. The connection with permanent water bodies is often temporary, thus enabling only a tiny proportion of the fry to leave the marsh before it dries out[2].

Adaptive responses of fauna

Given alternating wet and dry periods, aquatic animals, and particularly the invertebrates, have developed three basic types of adaptive responses:

- A very short life cycle during the wet period followed by resistant forms during the dry period: numerous invertebrates (*Anostraceace* - fairy shrimps, copepods, ostracods) can encyst themselves to survive the dry period. Mosquitoes can colonise temporary marshes due to rapid larval development and high survival of their eggs in the sediment. The eggs hatch with the flooding of the marsh if the temperature is sufficiently high.

- Exodus of adults towards other aquatic habitats: this is the case for certain diptera and coleoptera (eg. water beetles).

- Adaptation of adults to terrestrial life: eg. odonata, trichoptera, diptera.

In the absence of predatory fish, certain coloured or large crustacea *(Branchipus sp., Triops sp.)* become very abundant.

1 - Ramdani, 1986
2 - Poizat & Crivelli, 1997.

Amphibians

Amphibians are well-adapted to temporary marshes: their larvae and juvenile stages are strictly aquatic whereas the adults are terrestrial. Egg-laying normally occurs in spring during the wet period, and will succeed only if the flooded period is sufficiently long to allow all the metamorphic stages to take place up to the emergence of the adult. Rapid development and early laying are essential for successful breeding. In Andalusia, Spain, the Western spadefoot frog *(Pelobates cultripes)* takes advantage of the clement temperatures to lay between October and February, so metamorphosis is spread between March and June. Other species have less time to ensure their reproductive success. The laying of Parsley frog *(Pelodytes punctata)* begins in February and the metamorphosis occurs in April, the Stripeless tree frog *(Hyla meridionalis)* lays only from April onwards[1].

The variability of the flooding conditions (date, duration) and the small size of the often isolated populations, expose the species to high risks of local extinction. However, the risks are reduced by exchanges between populations living in different conditions, in pools or marshes which differ in their hydrological regime, and functioning as metapopulations*.

Toadspawn of *Bufo calamita* is wrapped around aquatic vegetation *(Callitriche brutia)*.

P. Grillas

1 - Nöllert & Nöllert, 1992

Birds

During the flooded period temporary marshes provide three types of habitats on which birds depend.

■ Feeding habitat

The abundance of resources, plants (leaves, seeds, tubers) animals (invertebrates, fish) and their availability, determine the use made of these marshes by herons, ducks, geese, rails and gulls. The drying out period in the spring, and flooding in the autumn provide particularly good feeding habitats for waders on migration and herons, by concentrating their prey into small areas of shallow water.

In the Camargue, teal *(Anas crecca)* feed in shallow marshes on seeds of *Cyperaceae* and oogonia of *Characeae*[1]. Large invertebrates, such as *Triops*, provide ideal foods for Little egret *(Egretta garzetta)*, Night heron *(Nycticorax nycticorax)*, Squacco heron *(Ardeola ralloides)* and Cattle egret *(Bubulcus ibis)*[2].

■ Breeding habitat

A dense vegetational cover is favourable to the nesting of moorhens, coot and even early nesting ducks such as mallard, when the flooded period is sufficiently long.

■ Resting habitat

The largest marshes can act as day roosts for wintering ducks (e.g. the marshes of Doñana or the Camargue). The presence of trees allows tree-nesting herons to roost in wetlands.

Mammals

In contrast to birds, wild mammals like rabbits *(Oryctolagus cuniculus)* and boar *(Sus scrofa)* mostly use the marshes in the dry period, whereas some domestic mammals (horses, cattle) make use of the abundant plant production during the wet period. Even though temporary marshes may be of secondary importance to these animals, the animal's impact on the wetlands is not negligible: trampling, scraping (rabbits), and rooting (wild boar) modify the soil structure and the distribution of seeds it contains, faeces provide fertilisation, and browsing and grazing contribute to the selection of plant species and the structure of the habitat.

1 - Tamisier, 1971
2 - Hafner, 1977

Wild boar commonly root in mud in search of food.

R. Cavignaux / Bios

Animals as vectors for the dissemination of plant seeds

Animals are important disseminators of seeds in temporary marshes since their movements from marsh to marsh carry seeds to sites suitable for their germination. Many seeds or spores are transported by animals, on their coat, on their hooves (wild and domestic ungulates), or on their feathers or feet.
A cubic centimetre of mud in a temporary marsh can contain up to a dozen seeds of different species. Darwin[1] noted the presence of aquatic plant seeds on the bodies of waterbirds. For example, in a sample of 36 waterbirds killed by hunters in a marsh in New Jersey, 28 of them were carrying a total of 89 seeds on their feet and especially on their wings[2].

Dissemination can also occur after passage through the digestive system of animals such as ducks, horses, coypus *(Myocastor coypus)*, rabbits, etc. Some seeds escape the action of the digestive juices and after excreting are still capable germinating. Partial digestion of the seeds' hard envelopes can favour germination by removing the inhibitors in the tegument (e.g. in *Scirpus*).

1 - *Darwin, 1859*
2 - *Vivian-Smith & Stiles, 1994*

J. Roché

The life of plants

The alternation of dry and wet periods is difficult for most plants to survive, whether they are aquatic, amphibious or terrestrial. This constraint is even greater because the timing of the two periods varies from year to year.

Flooding creates difficult conditions for photosynthesis in water due to the reduced availability of oxygen, carbon dioxide and light. Aquatic plants can overcome these limitations by anatomical and physiological adaptations: the presence of thin protective layers of tissue facilitates the absorption of the sun's rays (as there is no cuticle*, or palisade parenchyma*) ; tissues with empty spaces facilitate the internal circulation of gases (spongy parenchyma*) ; the use of soluble carbonates (rather than CO_2) as a source of inorganic carbon ; the assimilation of

Seeds of *Ranunculus peltatus* resist the summer drought until the marsh is flooded again.

nutrients by the leaves, and, finally, an internal supply of oxygen to the roots directly from the photosynthetic organs. The adaptive responses of aquatic plants to flooding depend on the duration of flooding, its depth, and the transparency and temperature of the water.

The period of transition between the wet and the dry period is often brief (a few weeks only). The amphibious species use this period to begin their development and can complete it on a humid or dry substrate.

The dry period also has its constraints: the high summer temperatures and wind increase the transpiration of the terrestrial plants and therefore their water requirements. In coastal wetlands or in endorheic basins, salinity is an additional, and particularly strong stress for terrestrial plants.

Under such difficult conditions, plants have developed a multitude of strategies for completing their life cycles, and for coping with the stresses of their changing environment.

A. Dervieux

***Callitriche truncata* produces bubbles of oxygen as it photosynthesises in bright light.**

The biological cycle: a way of life

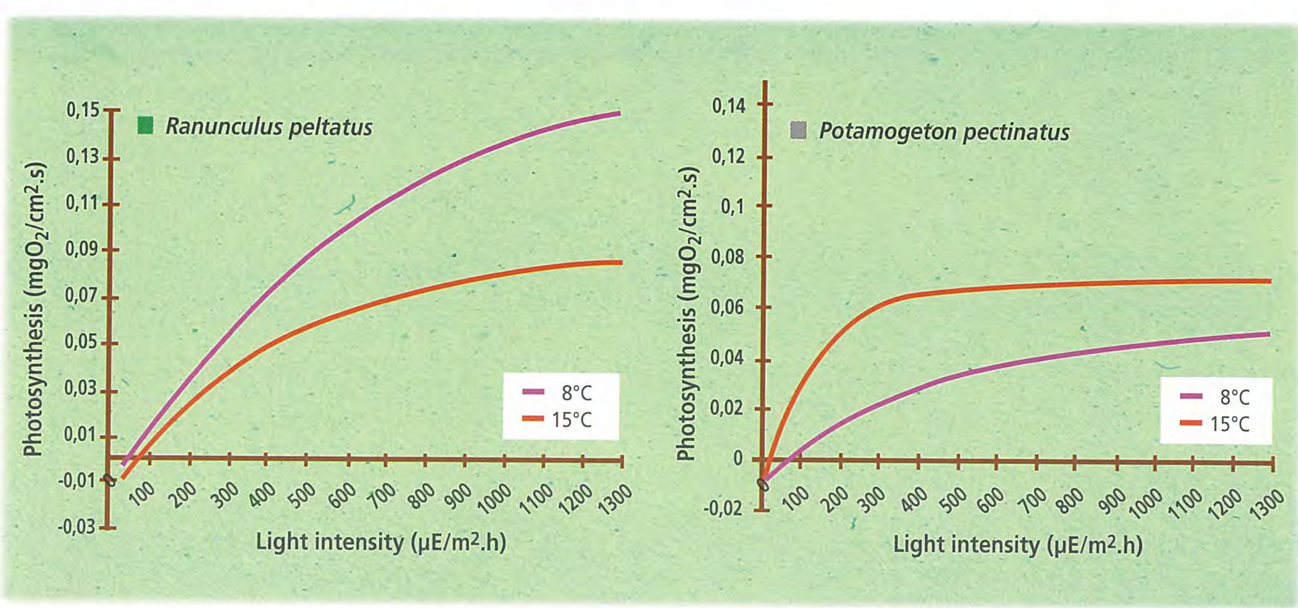
How annual species avoid stress

In the temporary marshes of Mediterranean France, 79 % of the plants characteristic of these habitats are annuals or biennials*[1].

Most species living in temporary marshes have responded to the diverse and intense seasonal stresses by developing a very short life cycle. This strategy allows the plant to avoid the most difficult periods for growth and to concentrate its annual cycle into the favourable period which may last from a few weeks to a few months. With the exception of amphibious species, plants have their active cycle, from germination to seed production, during either the wet or dry period. Thus they avoid the extreme ecological contrasts of the alternation between dry and submerged conditions. Most of the plants are, therefore, annuals and spend the difficult period as seeds or spores. Perennial* species dominate in more stable habitats such as permanent marshes where their life-form is an advantage in competition for space, light and nutrients.

The short period of flooding, which usually occurs in winter, forces the aquatic species to complete their life cycle rapidly. The aquatic plants increase their chances of success (the production of seeds) if they can use the whole of the flooded period and as a result, many do not have strict requirements for light and temperature. The strictly aquatic species *(Zannichellia sp., Callitriche sp.,* etc.) or certain amphibious species *(Ranunculus peltatus)* are able to germinate from autumn onwards if the marsh contains water, and reproduce at the end of winter or the beginning of spring. On the other hand, the species of the dry period, whether they are amphibious or strictly terrestrial, germinate in spring and reproduce at the end of spring (e.g. *Lythrum tribracteatum)* or in summer (e.g. *Pulicaria sicula).*

Photosynthesis, as measured by the quantity of oxygen produced, increases with light intensity and with temperature[2]. (*Ranunculus peltatus* grows in temporary marshes and *Potamogeton pectinatus* in permanent marshes).



1 - *Médail et al., 1996*
2 - *Volder et al., in press*

How perennial species adapt

Some perennial species occur in temporary marshes by using terrestrial or amphibious growth forms (helophytes), but they are never entirely aquatic. Their success is based on one of the following characteristics:

J. Roché

Lythrum tribracteatum.

- Surviving the contrast between several months of flooding and an extensive drought. Some aquatic ferns *(Marsilea strigosa, Pilularia minuta, Isoetes sp.)* and *Cressa cretica*, are capable of going into dormancy during unfavourable periods. *M. strigosa and P. minuta* develop during the wet period and their underground systems, well-protected from desiccation, survive the dry summer. Conversely, the life cycle of *Cressa cretica* is terrestrial and its root system goes into semi-dormancy during the wet period. If the seasonal contrast is lessened by humidity in the soil several helophytes can survive *(Phragmites, Scirpus spp.*, rushes).

- Functioning temporarily as an annual species: given very difficult conditions, the perennial organs of certain species disappear. As a result, the plant's continued survival is dependent on the seeds or spores, like an annual. This is the case for *Isoetes velata* whose perennial parts, similar to bulbs, die during the long summer droughts. The Isoetes therefore survives only by its spores.

- Colonisation from nearby habitats which are more secure; these species are not dependent on temporary marshes, which they colonise only during good years. This strategy is adopted by opportunistic species capable of rapidly increasing their populations and possessing a great aptitude for the dispersion of seeds. They can be aquatic (*Scirpus spp.* from permanent marshes) or terrestrial (*Limonium spp.* from saline grasslands).

The seed bank: a well-managed investment

The life of annual plants in temporary marshes is very precarious.

The data on the Camargue temporary marshes suggests that each generation has a different rate of germination - high in the youngest seeds, lower in the older seeds which are subjected to dormancy[1]. The most recent ones have a high rate of germination if the conditions of the first flooding are suitable. This category enables the rapid development of large populations. The older seeds germinate only with difficulty; they ensure the long term perennity of the seed bank and therefore the long term survival of the population.

Being eaten by herbivores, or repeated failure to germinate or to reproduce in an unstable environment, can cause the disappearance of a local population. The seed bank in the soil is therefore of great importance for the survival of a population in a particular site.

Two conditions ensure the perennity of the seed bank: the longevity of the seeds in the soil beyond one year, and a pattern of germination each year which does not use up the total seed bank. The number of viable seeds is the best way of estimating the size of the population. This measurement is far more accurate than counting plants, because a very abundant species may well be awaiting favourable conditions to germinate, yet be present above ground as a green plant in only small numbers.

The size of the seed banks, rates of seed survival, and their role in the functioning of plant populations in the Mediterranean marshes are not well understood. The available data is fragmentary but some information on the functioning of the seed banks in temporary Mediterranean marshes is becoming available.

Tens of thousands of seeds

An inventory of the seed banks in the first two centimetres of soil has shown the presence of tens to hundreds of thousands of seeds per square metre in Doñana (Spain), and the Camargue (France)[2]. The density of seeds depends not only on the spatial distribution of the different species (seeds of submerged plants are abundant in the centre of the marsh, seeds of amphibious plants on the edges) but also on the mechanisms and the agents of dissemination.

Temporary marshes have thousands of seeds waiting to germinate.

	Spain[2]	France[1]
Site	Doñana	Camargue
Density of seeds Thousands/m^2	320 - 530	40 - 800

1 - Bonis, 1993
2 - Grillas et al., 1993

Vertical distribution of seeds

The number of seeds decreases rapidly from the surface downwards. In two temporary marshes in the Camargue, 76-97 % of seeds and spores were found in the first four centimetres of sediment. These figures are very similar to those found in the Guadalquivir marshes or California (80 %) and are higher than those from wet grasslands (20-50 % of seeds in the first five centimetres). In Doñana and the Camargue, viable seeds have been found up to 10 cm below the surface.

The vertical distribution in the soil is the result of a number of phenomena: the extent of deposition of seeds on the surface of the soil, the slow rate of sedimentation in temporary marshes, the gradual migration downwards through cracks in the sediment, animal activity (trampling by cattle, uprooting by wild boar, scraping by rabbits), natural mortality, and consumption by different animals. In the Camargue, it is probable that predation by large numbers of granivorous ducks contributes to the decline in the stock of seeds at the surface, but this impact is probably very patchy and has not been measured.

In Australia, Brock and Britton studied the longevity of the seeds of species from temporary marshes in order to evaluate the possibility of using the dormant stocks of seed to restore drained sites. Samples of sediment containing 21 species were collected in 1982, and in 1993 were allowed to germinate. Only two species were able to germinate after being kept dry for 11 years: *Juncus articulatus* and *Myriophyllum varifolium*. In the site studied, the relict seed bank therefore did not enable the original vegetation to reconstitute itself after a long dry period. It is therefore sometimes necessary to sow seeds or transplant in marsh restoration projects[1].

Longevity of the seeds

The life span of seeds in the soil is not well-known. The seeds of *Callitriche truncata, Zannichellia pedunculata, Ranunculus peltatus* and the spores of *Characeae* and *Isoetes* remain viable for several years. In temporary marshes some species are commonly not seen for years and then suddenly appear in large numbers. Long-term viability has been noted in *Chenopodium album* (1,700 years), *Rumex crispus* (80 years), and for the spores of *Isoetes* and of *Marsilea*, using samples preserved for tens of years in herbaria. However, in natural conditions these rates of longevity may be rare. The survival of spores is probably better when they are dry and safe from predation than in a marsh subject to alternating wet and dry conditions.

1 - Brock & Britton, 1995

Germination: betting on the future

Germination is a very important stage in the life cycle of plants in temporary marshes.

Flooding conditions are variable and drying out dates are not predictable at the time of flooding, so the onset of germination represents a key "choice" for plants, since success is by no means assured. In this game the seed bank is the capital, the seeds that germinate are the stake, and the winnings are the number of seeds produced at the end of the season.

A strategy...

In an unstable and unpredictable habitat a species cannot risk all its capital at once, by allowing all the seeds to germinate as sooon as conditions seem favourable. Many different and unpredictable events during growth and reproduction could lead to extinction of the whole population if the entire seed production germinated. The seed bank allows the population to survive several consecutive years without reproduction, so in the long term it is better to maintain dormancy mechanisms which limit the percentage of the seeds which germinate at each flood event.

Seitre / Bios

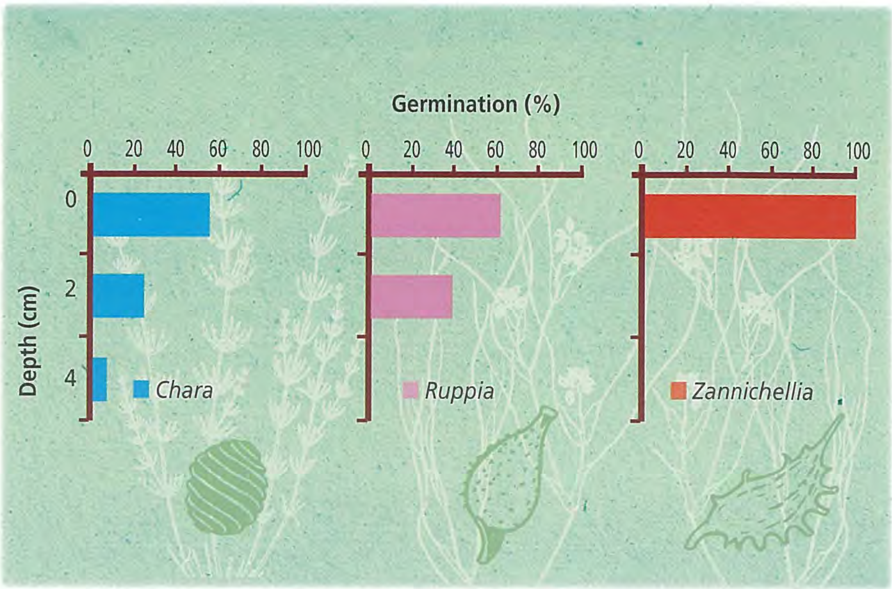
The arrival of Autumn rains triggers germination for many species.

... controlled by many factors

Temperature, humidity, light (intensity, composition), salinity, and oxygen all control germination. Different plants are affected differently by each of these factors, and by their interactions. The physiological state, and the primary and secondary dormancy of seeds, also limit germination.

Temperature plays a major role in the control of germination. There are basically two types of species: in those whose optimum temperature for germination is relatively low (aquatic and amphibious species), germination can take place in autumn or early spring with the arrival of the rains. The plant benefits from a relatively long period of growth in wet conditions. At the same time, the inhibition of germination by high temperature prevents the risk of late germination just at the point of drying out. The germination strategy of a number of species which reproduce in the spring *(Zannichellia, Callitriche, Ranunculus peltatus)* is based on two factors: flooding and temperature. The optimal temperature for germination is high in other species which are less dependent on flooding and can reproduce rapidly in spring *(Illecebrum)* or which flower in late spring *(Lythrum)*. It is not only the mean temperature which is important but also its fluctuations, which are sometimes necessary to break dormancy *(Rumex obtusifolius)*, occasionally in combination with light *(Lycopus europaeus)*.

An experiment on the seed banks of temporary marshes in the Camargue has shown that 99-100 % of seeds which germinate come from the first two centimetres of sediment. Those deeper down do not germinate or cannot produce seedlings sufficiently tall to reach the surface, because of the inadequate nutritive reserves in the seeds. This inactive part of the seed bank, older and probably in dormancy, can be reactivated by turning over the sediment.



The seeds lying in the top two centimetres have a higher germination rate than those lying deeper in the mud[1].

1 - Bonis & Lepart, 1994

Light is essential for the germination of *Zannichellia pedunculata*[2] or *Callitriche truncata*. The inhibition of germination by the absence of light is controlled by a photo-sensitive protein, phytochrome, in the seed coat. Burying of the seeds thus limits germination of these photo-sensitive species and contributes to the seed bank in the soil. These seeds could germinate if they are later exposed to light, for example, when an animal disturbs the soil.

Experiments in controlled conditions have shown that drying out followed by flooding stimulates the germination of seeds, but a change in temperature can sometimes modify the reaction[1].

The oxygen content of the soil declines rapidly during the flooded period due to the poor solubility of oxygen in water and the biological requirements for oxygen in the sediment. This decline, the implications of which are still not well understood, could be a signal for germination of the seeds of some aquatic plants, and an inhibitor for germination for terrestrial plants, or a limiting factor for their later development.

Salinity is a very important and very variable physical factor in coastal marshes. Most species are less tolerant of high salinity at the time of germination than during the rest of their cycle. Salinity can, at the time of flooding, be an important factor in the selection of the species which germinate, in relation to their tolerance. The impact of salinity during the drying out period is very important: for *Zannichellia pedunculata*, it decreases the optimal temperature for germination[3] and thus favours a rapid germination with the autumn flooding. The increase in salinity at the end of the spring also contributes to limiting germination, signalling the arrival of a dry period.

A. Dervieux

Clear water allows good light penetration and dense bottom growth.

1, 2, 3 - Van Vierssen, 1982

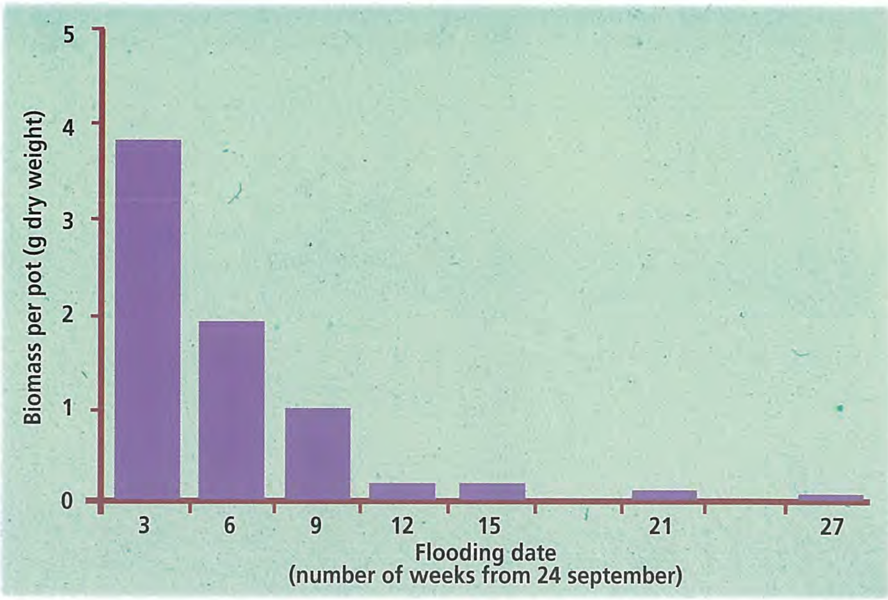
Growth: steady or rushed

The growth period of plants in temporary marshes differs between species.

It depends on the dry period in the terrestrial plants, the flooded period in the aquatic plants and the transitional period for amphibious plants. Many factors affect the growth of aquatic species.

The importance of the flooding date

Samples of sediment from a temporary marsh in the Camargue were subjected experimentally to 7 different flooding dates between the end of September and the middle of March. An interval of 3 weeks separated the first 5 dates, and for the last two it was 6 weeks. The plant biomass produced on each sample plot was harvested at the beginning of May, which is the time of maximum production and when water-levels drop rapidly. A striking decline in production occurred from the very beginning of the experiment: a delay of only three weeks in the timing of autumn flooding (24 September or 15 October) reduced the aquatic plant biomass in May by nearly half. This reduction in biomass resulted not only from the shorter flooded period for growth, but also the loss of a favourable period with warmer temperatures in early autumn. A longer flooded period in the warm spring can however compensate for low biomasses caused by late flooding in autumn for growth.

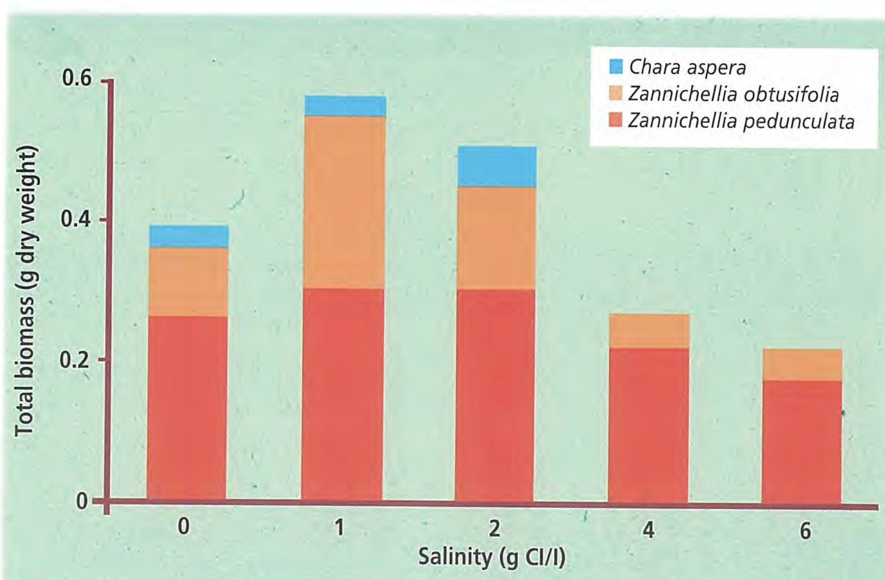


Early flooding increases biomass production. After Grillas & Battedou, in press.

The duration of flooding and the conditions of temperature and light during this period are the key factors. The longer the flooding, the more time the hydrophytes have to produce plant matter. Short periods of flooding therefore limit biomass production. In winter, reduced light and temperature are limiting; early flooding or late drying out in spring provide good conditions.

Water turbidity can also limit photosynthesis, and therefore the production of plant matter. If the sediment is put into suspension by the churning effects of wind, or the passage of animals, the amount of light available in the column of water declines considerably, and this can affect the development of submerged plant communities[1]. The effect of turbidity is greater when the water is deep.

Plants are more tolerant to salt during growth than during germination. The consequences of being exposed to salt are different according to the species: *Althenia filiformis, Chara canescens* and *Lamprothamnium papulosum* are very tolerant. The *Ruppia* species and especially *R. cirrhosa* tolerate concentrations between 1.5-60 ppt of total dissolved salts. In other species production is reduced sharply by even low concentrations of salts *(Callitriche truncata, Chara vulgaris)*; some species never occur in sites exposed to salt *(Isoetes pl. sp., Hippuris)*. The impact of salinity depends on the amplitude of the annual fluctuations and particularly its level in spring, the most favourable period for growth. At high concentrations, intolerant species are killed. A very small number have their growth stimulated by salt *(Arthrocnemum, Salicornia)*.



Submerged plants react to salinity in different ways. After Grillas *et al.*, 1993

1 - Duarte et al. 1990

Reproduction: restocking the seed bank

A. Dervieux

Oogones of *Chara*.

Vegetative reproduction by propagules* such as tubers and cuttings is the dominant form of reproduction in permanent marshes, whereas sexual reproduction is by far the commonest form in plants of temporary marshes.

Apart from the genetic recombination that it brings, and therefore the possibility of long term adaptation, the seeds or spores produced by sexual reproduction are in general more resistant to variations in habitat conditions. Seeds have thick teguments which protect them against desiccation and predators, and they can survive several years in unfavourable conditions, whereas vegetative propagules cannot.

When to invest?

Submerged plants must produce their seeds during the wet period in order to ensure their reproduction, because the plants die quickly when exposed to air. In a marsh that dries out rapidly the submerged plants are characterised by early reproduction. In North Africa, the sexual reproduction of *Ranunculus peltatus* and *Callitriche hermaphroditica* begins as early as February. In marshes on the north coast of the Mediterranean, *Tolypella glomerata, T. hispanica* reproduce early, February-March, and many others *(Zannichellia pedunculata, Z. obtusifolia, Ranunculus peltatus, Ruppia drepanensis)* in early April or May. Different species of *Chara* reproduce between May and July but these species are found principally in areas which dry out late. Some other species can have two or three flowering periods if the hydrological conditions allow it *(Zannichellia pedunculata).*

Amphibious plant species generally reproduce later than the submerged species, after a lowering of the water level (e.g. *Damasonium polyspermum).* Terrestrial species flower between the end of spring *(Lythrum tribracteatum, Limonium virgatum)* and autumn *(Kickxia commutata, Pulicaria sicula).*

With what result?

The number of seeds produced is very variable from one species to another, and from one year to another. *Cressa cretica* only produces a few seeds per m^2 in contrast, for example, to several tens of thousands produced by *Callitriche truncata.*

The difficulties of pollination in an aquatic habitat

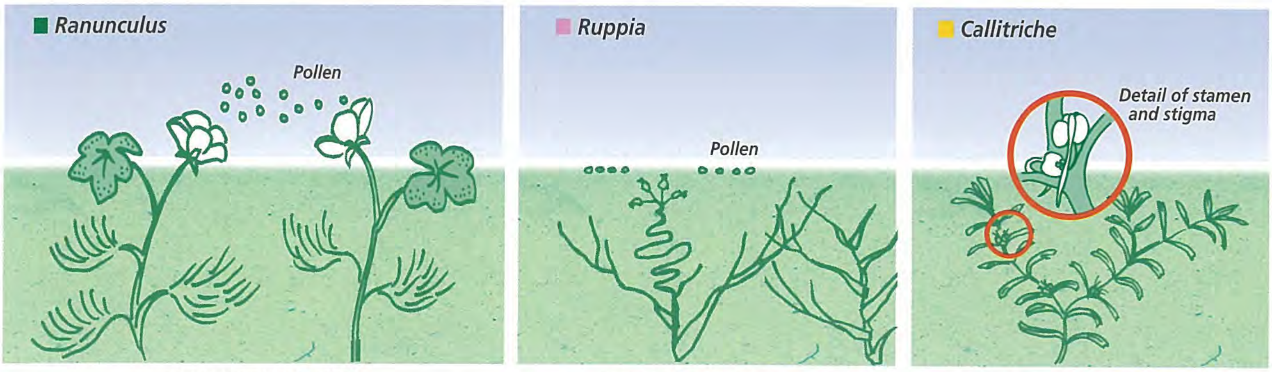
Pollination is much more difficult in water than in air because of the problem in transporting pollen to the stigmas (low fluidity in the liquid medium, absence of pollinating insects). As a result the plants have developed several different strategies:

- Looking for air: in 90 % of aquatic angiosperms* pollination is aerial. In order to reach the surface of the water submerged plants must grow sufficiently high, and this depends on the depth of the water. In *Ranunculus peltatus*, the flowers are carried above the water where their stability is ensured by solid floating leaves, very different to the highly indented submerged leaves. The pollination of the female flowers of *Ruppia cirrhosa* occurs at the surface of the water where the male flowers detach themselves from the plant and drift; the female flowers are carried to the surface by a long peduncle which retracts after fertilisation.

- Autofertilisation: pollination underwater is rare for freshwater angiosperms, but is found in monocotyledons (e.g. *Zannichellia, Najas)* and in some dicotyledons* *(Callitriche pro parte)*. Most of these species are autogames, i.e. the female flower is fertilised by the pollen of the same flower. Several mechanisms are used to help the stamens to meet up with the stigmas, for example the curving of the stigmas towards the stamens *(Callitriche)*, or the production of an air bubble which pushes the pollen towards the stigma *(Ruppia maritima, Zannichellia pedunculata)*.

- Aquatic gametes. Pollination underwater is the rule in pteridophytes* *(Isoetes, Marsilea, Pilularia)* or algae (charophytes), as they have swimming aquatic gametes.

Three methods of pollination used by aquatic plants.



AERIAL POLLINATION
Cross-pollinating

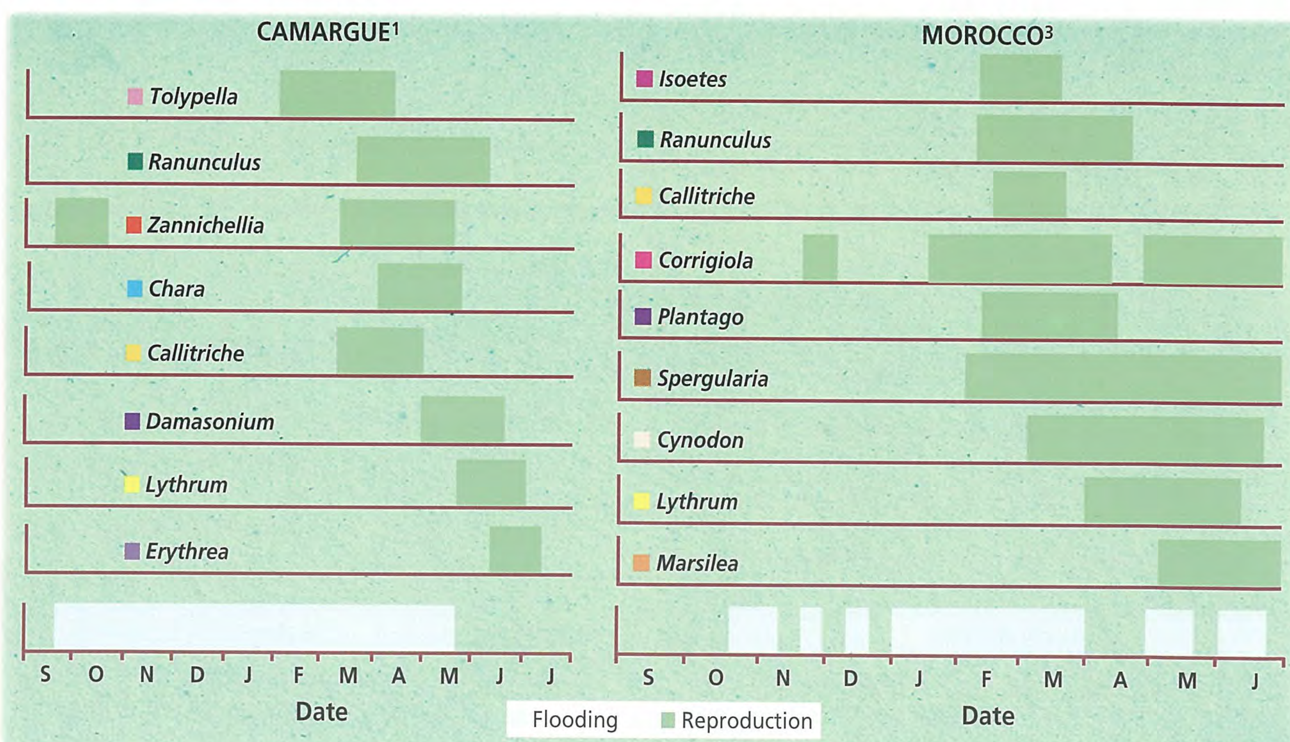
SURFACE POLLINATION
Cross-pollinating

UNDERWATER POLLINATION
Self-pollinating

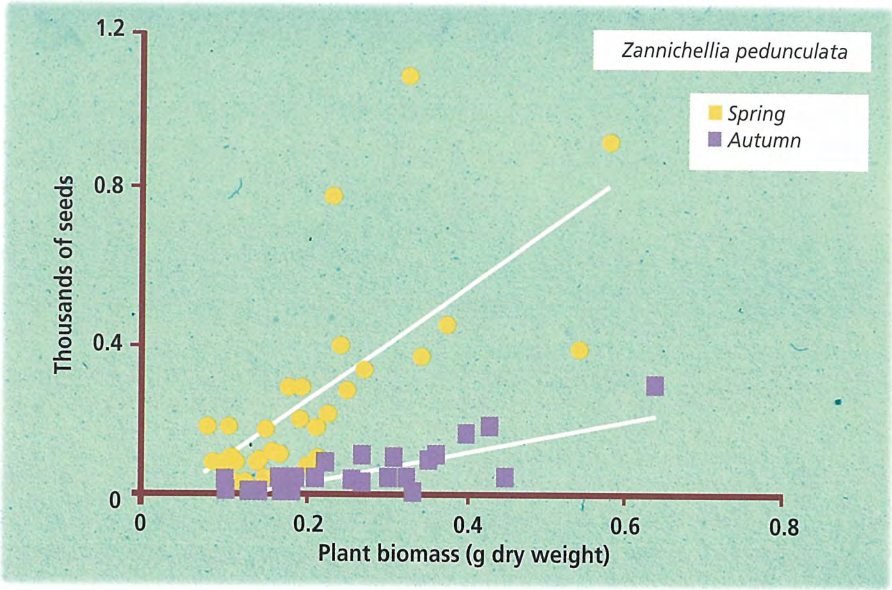
For most annual species, particularly those in temporary marshes, the number of seeds produced varies with the size of the plant[1]. The potential seed production, therefore, fluctuates greatly from one year to another, according to the conditions of germination and growth. For submerged species, potential seed production is realised only if the marsh does not dry out too early, and as a consequence the size of the seed bank varies greatly from year to year. These fluctuations are not synchronous between species. The reproductive success of the late species *(Chara sp.)* is more variable than early species.

Other factors affect the production of seeds directly or indirectly. Intra- and interspecific competition affects the investment of plants in sexual reproduction: the number of seeds produced by a plant of *Ranunculus peltatus* declines with plant density[2]. The number of stems of *Chara aspera* carrying oospores is significantly smaller when covered by *Ranunculus peltatus.* Grazing by herbivores indirectly limits sexual reproduction by its impact on the biomass, and invertebrates can completely halt reproduction of *Cressa cretica* by laying eggs in the flower buds.

Timing of reproduction in a few temporary marsh plants.

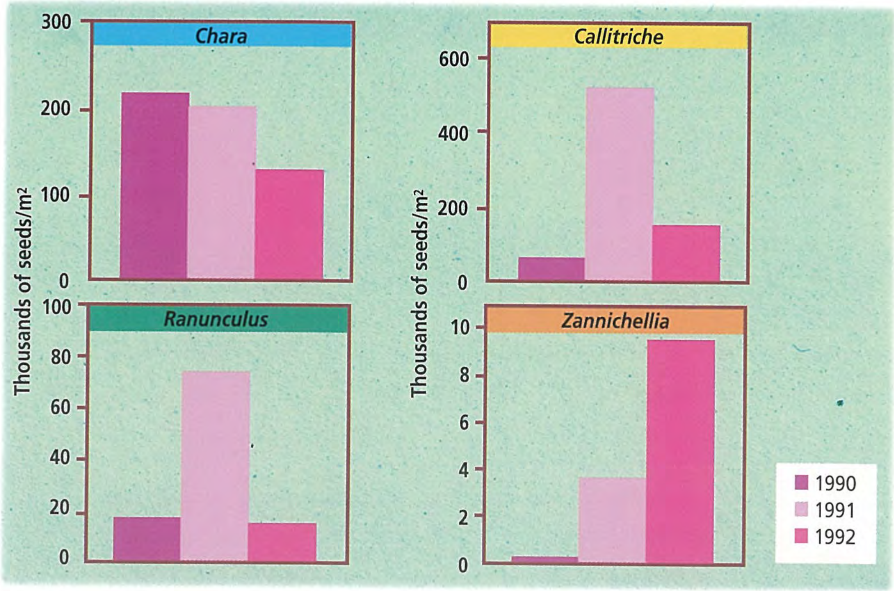


1 - *Bonis et al. 1995, Grillas & Battedou, in press.*
2 - *Volder et al., in press*
3 - *Dupuis, 1988*



Zannichellia pedunculata **produces many more seeds in the Spring than in the Autumn. After Grillas *et al.*, 1991.**

Environmental stresses can also modify the investment in reproduction (the number of seeds produced per unit of biomass). Exposure to salt (in the range 0-18 g/l) reduces the investment in reproduction of *Chara contraria*, whereas it increases the investment in *Chara canescens*. The production of seeds is a good indicator of a species' tolerance or intolerance to salt.



The number of seeds produced varies from year to year and between species. After Bonis, 1993.

Dispersal: to leave, or not to leave?

Faced with the spatial isolation of temporary marshes dotted around the Mediterranean and often fragmented within one region into "pools" or small marshes, what dispersal strategy should plants adopt ?

Should they look for better living conditions elsewhere and disseminate over a long distance or try to survive in the same place, and keep the seeds in a small area? Each strategy has its risks and its benefits.

Dispersal within the parental site guarantees, at least in the short term, a habitat which has already proved suitable. On the other hand, in the long term with no long distance dispersal to other sites the population is exposed to the risk of total extinction in the case of disturbance, and to the risk of a decline in vigour as a result of isolation inbreeding depression. The latter risk is greater in small populations.

Long distance dispersal, on the contrary, reduces the risk of local extinction by the input of new genes and offers the possibility of colonising new sites. Colonisation poses relatively few problems in the large wetland complexes, but it is less likely to be successful in the case of isolated and small sites.

A. Dervieux

The aquatic form of invertebrates cannot escape when the marsh dries out.

Rabbits disperse seeds through their faeces and on their fur.

Isoetes sp. and *Ranunculus* section *Batrachium* have limited dispersal strategies: one is by spore production in the soil at the base of the leaves, the other in *R. peltatus* for example, is by the bending of the flower peduncule after pollination, which pushes the seeds into the soil in the immediate proximity of the parent plant.

On the other hand *Callitriche truncata, Mentha aquatica* and *Alisma sp.* produce many floating seeds which disperse easily on the water surface. In some species the seeds sink immediately, but dispersal over a short distance is possible when, at the next flooding of the marsh the seedlings float to the surface after germination (e.g. *Rumex, Callitriche).* Dispersal by wind is also used by *Eryngium sp.*,when the whole plant rolls up and is blown with its seeds. The dispersal role of rabbits, by their faeces, has been shown in California in a similar habitat to Mediterranean temporary wetlands[1].

Each species thus uses different means of dispersal, some even using several strategies and dispersal agents simultaneously. This is the case with *Isoetes*, whose spores can either go into the soil or be dispersed at a distance by birds, and *Ranunculus*, whose akenes* are left next to the parent plant but have a hook which facilitates transport by animals. Some species like *Spergularia salina* produce two types of seeds, morphologically different (with or without wings) corresponding to the two different dispersal strategies[2].

1 - Zedler & Black, 1992
2 - Redbo-Torstensson & Telenius, 1995


C. Perennou

Structure and dynamics

The biology of plants, and their survival strategy in the temporary marshes, has shown how they can adapt to difficult conditions.

The distribution of species is a response to the spatial variation of the constraints they have to face. At a regional level, factors such as salinity, water pH and the nature of the substrate need to be known in order to understand the distribution of the plants and explain differences in floristic composition from one marsh to another. The pH and geology play an important role in inland marshes, as does salinity in the coastal marshes or the endorheic basins. At a local level, other factors control the suitability of a habitat. The flooding regime, which is linked to topography (particularly the slope of the edges of marshes) is the principal factor. These factors combine to produce the ecological gradient (humidity, salinity, etc.) which determines the vegetation:

Ranunculus peltatus is a common white-flowering plant of Mediterranean marshes.

aquatic in the centre of the marsh, amphibious on the edges, and terrestrial on the periphery. The biotic factors (competition between species, grazing, different disturbances caused by animals, etc.) also play a role, and vary from one site to another.

Plant communities are temporally unstable. The ecological conditions fluctuate from year to year, and benefit one group of species one year and another group the next; the turn-over of species is high. When ecological conditions are stable for several years, they favour the expansion of one or more species; these spread as quickly as the dynamics of their populations allow.

Plant community dynamics are linked to the ecological conditions. They depend on the colonising ability and the population dynamics of the different species, which result from the principal biological features of each (longevity, growth form, tolerance to different environmental factors, reproductive strategies, etc.). Chance also plays a role in the spatial and temporal dynamics of plant communities, particularly because certain events (major habitat disturbance) or certain parts of the biological cycle of the plants (seed dispersal) are unpredictable.

J. Roché

Population dynamics are patiently assessed using quadrats.

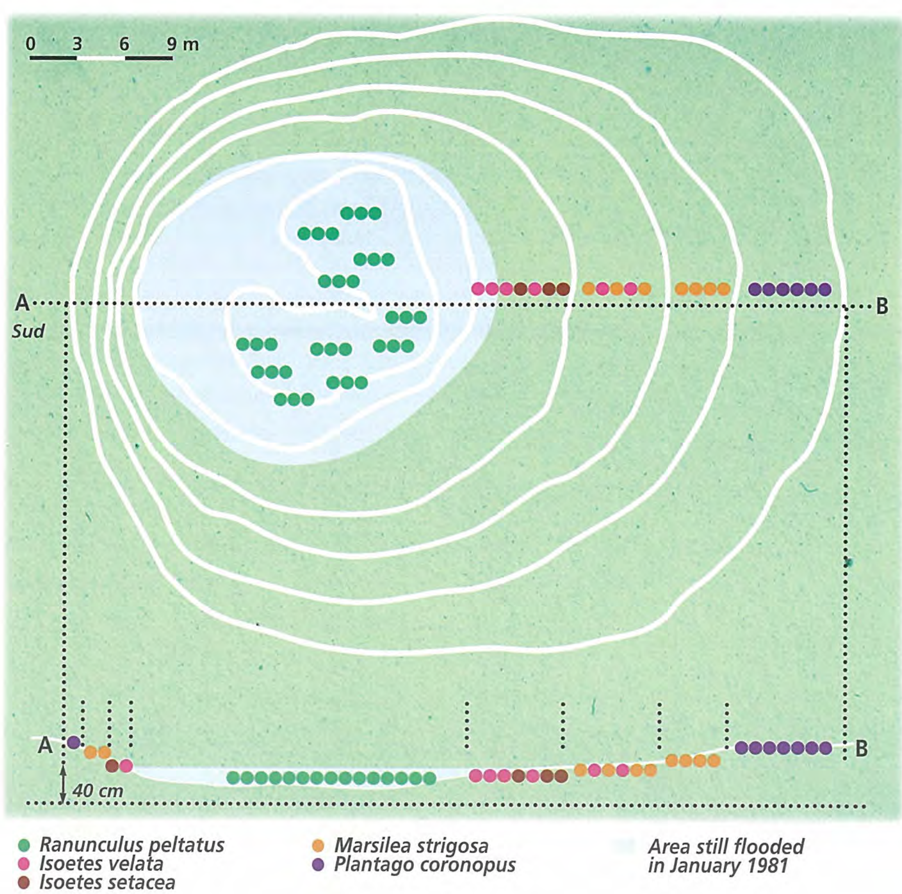
Zonation

The positioning of the plant communities in concentric circles or parallel to the edge of the marsh underlines its topography.

This pattern results from several phenomena, the most important of which is the existence of ecological gradients on the edges of marshes: a gradient of depth, the duration of flooding/drying out, the granulometry of the sediment, temperature, light, and salinity. Each species can make use of a specific zone within the gradients. Unlike permanent marshes, where the zonation of the vegetation is determined principally by the depth, light attenuation, or the abundance of nutrients, here the zonation depends principally on the duration and timing of flooding.

Other factors also contribute to the zonation of the vegetation such as the thickness of fine sediments (clay, silt) rich in nutrients, and the abundance of organic matter, both of which are higher in the centre of the marsh than on the edges.

The slope of the marsh edge strongly influences the spatial distribution (zonation) of the vegetation: a gentle slope favours a diversity of micro-habitats for the plants, whereas a steep slope leaves little place for the species which occupy an intermediate position on the topographic gradient.



The different plants species tolerate different flooding regimes, and distribute themselves according to the contours of the marsh. After Boutin *et al.* 1982.


J. Roché

The edges are already cracking but the centre remains wet.

Competition reinforces zonation. It exists between plants of the same species, as well as those of different species; the intensity of this competition increases with the quantity of plant biomass (total or per species). The perennial and emergent species are generally more competitive than the annuals, and those with a strong vegetative reproduction can limit the expansion of annuals. For example, *Juncus gerardi, Scirpus maritimus* or *Isoetes setacea* can limit or prevent the development of annual aquatic plants or amphibious plants by occupying the space available. Competition for nutrients probably plays an important role in spring when biomass is increasing quickly, and the concentration of nutrients is at its lowest. It is likely to be intense in oligotrophic* sites where nutrient salts are not abundant.

Wild and domestic animals disturb competition between plants and modify the structure of the vegetation. Wild animals can exert grazing pressure on temporary marshes at all stages. During the flooded period herbivorous ducks and coypus consume submerged and emergent plants respectively. Grazing by ducks occurs principally in winter when their densities are high and temporary marshes are an important feeding habitat.

Wild boar use temporary marshes during the drying out and the flooding period when they feed in damp and lightly flooded ground. They eat the fleshy underground parts of amphibious and emergent plants (roots, rhizomes, tubers).

Domestic herbivores feed essentially on the aerial parts of amphibious species and helophytes. Only the most hardy breeds of cattle and horses go into the marsh when it is flooded. Sheep and goats graze dry wetlands only.

Moderate grazing by animals provides several advantages for submerged plants: it keeps the vegetation open, favours better light distribution in the marsh, exports a part of the plant biomass and slows down the succession to a terrestrial ecosystem. With colonial species *(Scirpus sp.*, reeds, etc.) present, which tend to close in and impoverish the submerged communities, extensive grazing can maintain diverse plant communities. The loss of extensive grazing in numerous wetlands all over Europe has led, over the years, to an invasion of these habitats by trees (elm, *Ulmus*, ash, *Fraxinus* etc.) and species-poor communities *(Scirpus spp.*, rushes).

Vegetation dynamics: annual and pluriannual cycles

The alternation of a dry and a flooded period causes considerable modifications in the plant communities, not only during the year, but from one year to the next.

At flooding the plants in the marsh react in different ways:

- Hydrophytes and amphibious plants germinate.
- Terrestrial annuals, which have survived the summer, die (soda plants, grasses).
- Terrestrial perennials and amphibious plants (glassworts, rushes) try to survive using different adaptations to the stress due to flooding (provision of oxygen to the underground parts of the plant, dormancy, etc.).

The aquatic period

The dynamics of the vegetation now depend principally on the flooding regime and, in particular, on these three characteristics: the duration of flooding, the dates of the beginning and the end of flooding.

A sufficiently long period of flooding is essential for the completion of the life cycle of aquatic plants, from germination to seed production *(Zannichellia pedunculata, Callitriche truncata).* Short flooding periods tend to favour the submerged plants with the shortest life cycles.

The flooding date can also influence the composition of the plant communities. In the short term, flooding initiates germination of aquatic plants and marks the beginning of their annual cycle. Germination is controlled by temperature and light conditions. At low temperatures (<10°C) germination is slowed down sharply. At high temperatures (>25-30°C), some aquatic species, which reproduce early, like *Zannichellia pedunculata*[1] or *Callitriche truncata* no longer germinate.

The periods most conducive to germination are, therefore, autumn or spring, when the plants benefit from the favourable conditions of insolation and temperature. Different species are favoured by different dates of flooding, and they will be at an advantage over the others. In the long term, the date of flooding has effects on the restocking of the seed bank of aquatic plants. The earlier the flooding date the greater the plant biomass produced[2] and the larger the seed production. Species with large seed banks are endowed with a potential that can be fulfilled during favourable years. In unusually dry periods terrestrial

1 - Van Vierssen, 1982
2 - see figure page 44

plants will temporarily invade the marshes. This is how woody plants of the Mediterranean maquis such as *Pistacia lentiscus*, and *Cistus spp.*, manage to colonise temporary marshes during dry years but are killed by flooding in wet years.

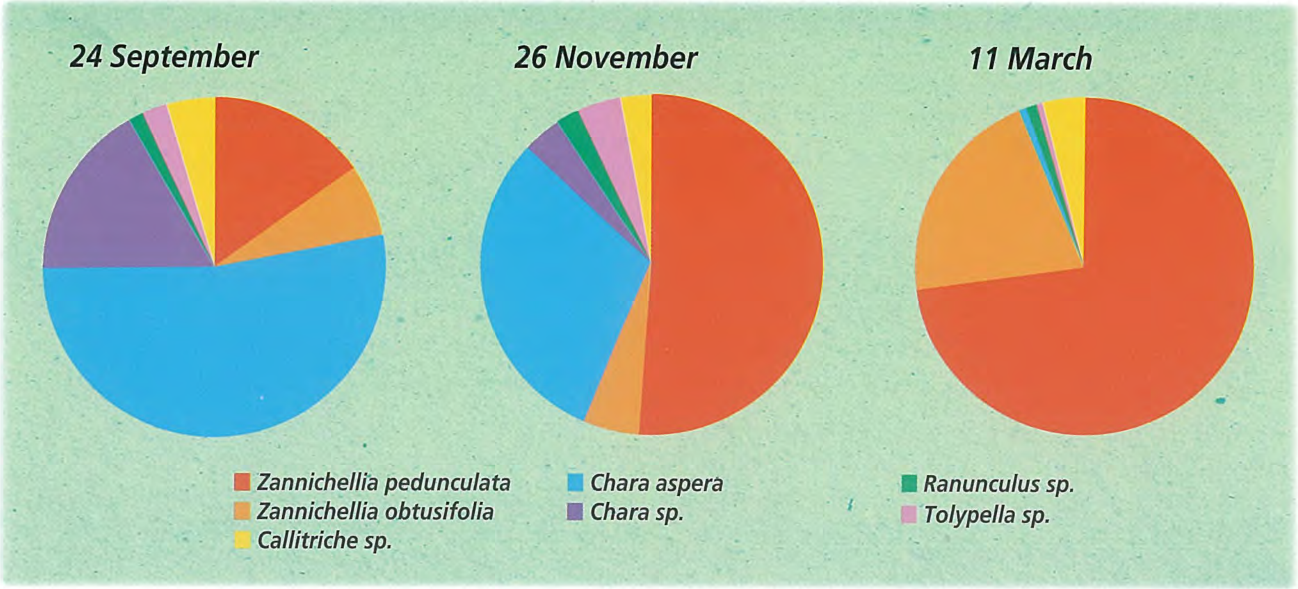
The drying out period

With the gradual lowering of the water level, amphibious plants begin to develop, and the biomass of aquatic plants declines as individuals die from exposure and lack of space. For aquatic plants it is essential to complete the production of seeds during this period or their reproduction will fail and the seed bank will become exhausted.

Aquatic plants have an interest in reproducing as early as possible in order to limit the risks of this drying out period. Its ability to reproduce early, from autumn onwards if the flooding is adequate, explains, at least in part, the abundance of *Zannichellia pedunculata* in the Camargue and coastal marshes. The reduction in the water column together with a rise in daily temperature leads to a compressed growth cycle and early reproduction[1].

It is, however, generally agreed that early reproduction has a cost in terms of survival and production, and ultimately reduces the total number of seeds produced in a good year. When flooding occurs late in spring, species with late reproduction *(Chara sp.)* have an advantage over others which reproduce early *(Tolypella, Zannichellia)*.

An experiment shows that the species composition in the following April depends on the date of flooding. After Grillas, 1992.



1 - Barko and Smart, 1981

The terrestrial period

With the arrival of the dry period, amphibious plants which have germinated in the flooded period (e.g. *Ranunculus spp., Alisma ranunculoides, Damasonium polyspermum)* develop rapidly and begin (or complete) their reproduction.

The dry period suits the terrestrial plants. The annuals complete their cycle very rapidly after drying out (e.g. *Bromus, Hordeum* or *Trifolium, Corrigiola)* and the perennial plants flower in the course of the summer (e.g. *Cressa cretica, Limonium vulgare, Plantago coronopus)* or in the autumn.

Although the water content of the soil is important, *Ranunculus peltatus* is capable of germinating and completing its life cycle in dry, as well as flooded, conditions. If the dry period occurs early in the season, this species can replace the aerial parts, stems and leaves, which are adapted to the aquatic period (the leaves are long and strip-like, spongy parenchyma), by whole new leaves adapted to terrestrial habitats, thus ensuring seed production equal to that obtained in aquatic conditions.

The survival of plants during the dry period varies in different species, and according to the capacity of the soil to retain humidity. On sandy, highly permeable, dry soils in the summer the terrestrial vegetation is limited to a few transient small species adapted to the very unstable conditions (e.g. *Tillaea muscosa, Aira capillaris, Briza minor, Bromus hordeaceus, Hordeum marinum).* Conversely, on the silty soils, rich in organic matter, the water content can remain adequate for the survival of perennials. The sediments of coastal marshes are often fine enough to support vegetation during the dry period, but salinity can become a serious additional constraint. The summer vegetation of brackish marshes includes for example, *Suaeda maritima, Suaeda splendens, Scirpus maritimus, Cressa cretica, Aeluropus littoralis* or *Frankenia pulverulenta.* On skeletal soils with high permeability, the summer drought severely limits terrestrial vegetation.

The full annual cycle is not necessarily completed in all sites every year. Depending on the climatic and local conditions, the vegetation of the terrestrial or the aquatic period may be very limited, or even completely absent. As a consequence, the cycles of vegetation can change from one year to the next, so that terrestrial vegetation dominates during dry years and then dies back in wet years when aquatic communities gain ground.

Temporary seasonal marshes: islands in the landscape

From a landscape point of view, temporary marshes are patches in the countryside. Seen from above, they appear as "islands" set in terrestrial habitats with which they contrast to a greater or lesser extent: forests, maquis, grasslands, and crops.

The animal and plant populations persist only if the balance between the capacity of the species to colonise, and the risk of local extinction, is positive.

The perennial seed bank reduces considerably the risk of local extinction by maintaining the populations at high levels, and buffering the effect of unfavourable years.

Exchanges between sites take place essentially in the form of seeds (or spores) or pollen. The intensity of the exchanges between sites depends on the distance between them, the permeability of interstitial habitats to seedlings, the mechanisms of dispersal and the number of potential vectors available for transport[1]. Seeds can be transported by water, wind, ants, mammals, or birds. Pollen is transported by wind, water (as in cryptogams with swimming gametes like *Isoetes sp.* or *Pilularia sp.)* or by insects.

A. Dervieux

Horses carry seeds and spores and assist dispersion.

1 - Van der Pijl, 1982

In coastal wetlands, the large number of sites in a relatively small area (e.g. the pools and marshes in the Camargue), the hydraulic connections and the abundance of wild and domestic animals favour these exchanges. In marshes or temporary marshes which are more isolated, long distance exchanges are probably very limited. Waterbirds, however, can be very important vectors as they travel so quickly between marshes.

For many reasons, temporary marshes can be considered real islands in the landscape.

The ecological isolation of the temporary marshes makes distant dispersal to a favourable site most unlikely. In addition, the flora of temporary marshes often have poor dispersal strategies, such as *Isoetes* sp. with its underground spores or *Lythrum hyssopifolium,* which keeps its seeds on the plant. This behaviour is characteristic of flora from other isolated habitats, such as real islands in the sea or wetlands in desert regions.

When the isolation is broken

Due to their isolation, temporary marshes contain original planktonic crustacea because these large and tasty species do not have any serious predators apart from birds like herons or Gull-billed terns *Gelochelidon nilotica.* The connection of temporary marshes with permanent water following rain or the construction of hydraulic infrastructures can endanger these populations. In the Camargue, for example, the construction of an agricultural drainage canal enabled the colonisation of temporary marshes by sticklebacks *Gasterosteus aculeatus.* Monitoring of the crustacea showed that predation by fish affected the large planktonic species

P. Garguil / Bios

Gasterosteus aculeatus.

(Daphnia magna, Simocephalus vetulus, etc.) severely, but had no effect on the populations of smaller species[1]. Halting the isolation meant that the zooplankton community lost, by a rapid process of extinction, the species which are most typical of temporary marshes.

1 - Pont, Guillot & Crivelli, 1991

J. Roché

Conservation and management

Temporary marshes provide very particular conditions in which to live, and many plants show specific adaptations to them.

In countries like Israel the majority of endemic plants live in temporarily flooded zones. Certain groups of fauna, like the Branchiopod crustacea, are dependent on temporary marshes, and their diversity reaches the highest levels recorded in the Mediterranean region[1]. The loss of these refuges, and with it their species, therefore results in an important loss of biodiversity.

A restored marsh in the Nestos Delta, Greece.

1 - Brtěk & Thierry, 1995

A delicate balance

The temporary marshes which exist in the Mediterranean region today are often the result of a precarious balance between nature and human intervention.

Unlike other wetlands, temporary marshes are not highly esteemed by the public, most probably because they are not spectacular for animals.

In some cases, important sites for fauna or flora can be destroyed by agriculture before their value is even recognised. This is the case for the small, irregularly flooded, shallow marshes, which disappear without anyone noticing.

These wetlands, often shallow and with a hydrology which is unpredictable, can be filled in rapidly. In natural conditions, submerged aquatic plants tend to be replaced progressively by competitive emergents like *Scirpus spp.* and reeds, which are themselves replaced later by woody terrestrial vegetation, thickets (e.g. of *Cistus spp., Phillyrea angustifolia)*, or copses of ash or elm. This succession threatens the survival of temporary wetlands in a number of Mediterranean regions. The extensive grazing traditionally practised in these temporary marshes reduced or halted succession by restricting the development of invading helophyte plants and the resulting accumulation of organic matter. A change in the balance between grazing and natural plant dynamics can threaten the very survival of the temporary marsh.

Disappearance and degradation of temporary marshes

All around the Mediterranean there are numerous examples of the loss of this habitat. In Malta, rock pools have disappeared due to urbanisation. In Israel, Spain, and France numerous marshes have been drained and cultivated. In Morocco and in the whole of the Mediterranean region these marshes have been destroyed in the fight against malaria. Rubbish dumps, overgrazing, permanent flooding and eutrophication have led to their degradation. These varied threats are present in most Mediterranean countries.

Multiple threats

Temporary marshes are subject to most of the threats faced by wetlands.

In 1948, in the region of Cadiz, Spain, 18 of 43 wetlands were permanent, and 25 seasonal, covering an area of 8 700 ha. By 1991, only one was permanent, 6 were semi-permanent, 13 seasonal and 23 had been dried out[2].

Hydrological disturbances, eutrophication from agricultural run-off, chemical pollution from pesticides, industrial and household effluents or invasion by exotic plants carried by water, are all factors which upset the functioning of the marshes. Increasing the area of land under agriculture, urbanisation for industrial uses, the tourist industry, and the expansion of towns, have all led to the disappearance of these temporary wetlands[1]. Given the small amount of available information on these habitats, it is often hard to appreciate the speed with which they are disappearing.

Temporary marshes are also exposed to specific disturbances, or to those which are of particular importance for these habitats.

Hydrological disruptions and their consequences

The communities living in temporary marshes have been shown to be very sensitive to the water regime. All actions which lead to its disruption can therefore have a major impact, and their effects take on different forms:

■ Reduction in the length of the flooded period

The pumping of water from marshes lowers the water table. This tends to reduce the frequency and the length of the flooded periods, because it causes a hydrological deficit which needs to be compensated by rainfall and run-off. In coastal marshes pumping freshwater from the dunes often has this effect, and the water table is then exposed to infiltration by saline water.

The fragility of populations

The range of some of the plants of temporary marshes is so small that their very survival is threatened. For example in France, *Isoetes setacea* is found only in two sites near Agde, and *Marsilea strigosa* is only found in the département of the Hérault. In Europe *Teucrium aristatum* exists in Spain and in one site in France (Crau), whereas *Ranunculus revelieri* is only found in France (Maures, Estérel) and in Italy (Sardinia).

1 - See n° 5 in the MedWet series
2- Corona, 1991

Examples of over use of underground water for agricultural purposes can be found in Spain, in Doñana and the Tablas de Daimiel.

If the frequency of flooding declines, its duration generally does so too. This process contributes to the disappearance of certain plant populations by competition with other terrestrial species, by the lack of seeds in the seed bank, or by too-frequent failures in reproduction. In this way the change from an aquatic habitat to a terrestrial habitat, with the invasion of woody plants, is favoured.

The decline in the duration of flooding leads to the appearance of a community of terrestrial and amphibious species which replaces the aquatic ones. Annual species whose reproduction is late *(Chara aspera, Potamogeton pectinatus)* will be more threatened by a shortening of the flooding period than those which reproduce earlier *(Tolypella glomerata, Callitriche truncata)* because their chances of producing seeds are reduced. This type of disturbance can reduce the biomass and the frequency of occurrence of species over the years and, therefore, their chances of survival.

With terrestrial and amphibious species, the impact of this reduction is variable and is largely dependent on how long the soil remains damp. Invasion by perennial herbaceous or woody species like ash, elm, *Phillyrea angustifolia* and rockrose *(Cistus spp.)* then becomes possible, but is accompanied by a considerable decline in the species richness of the vegetation and of the characteristic species.

A. Dervieux

Early dessication reduces seed production.

■ Increasing the duration of the flooded period

This disturbance has several causes: uncontrolled flooding by run-off from agricultural drainage (e.g. ricefields), or planned flooding to increase grassland production, or to provide wet areas for game birds or waterbirds in general.

If the flooding is permanent, or nearly so, the characteristic species of temporary wetlands disappear and are replaced by a few very productive, submerged *(Potamogeton pectinatus, Myriophyllum spicatum)* or emergent species *(Scirpus maritimus, Typha spp.)*. This is the case in the Camargue with the summer flooding of hunting marshes. *Potamogeton pectinatus* is particularly encouraged in hunting marshes, as it provides an important biomass of plant matter (seeds, bulbs, leaves) much appreciated by duck.

The shallow water associated with brief summer dry periods encourages helophytes[1]. When the colonial, perennial species dominate, the plant communities become commonplace and their diversity declines. Also, these species, highly productive in temperate climates, can be a problem in canals and lakes.

Grazing

Grazing as such is not a threat for temporary marshes, and it has probably contributed to their conservation for millennia. If the grazing pressure is too heavy, however, it can have disastrous consequences for nature conservation. In Mediterranean marshes heavy grazing often reduces the vegetation cover, rare species disappear, and the richness of the site declines. In contrast, in the north of the Mediterranean region there are examples of marshes where the loss of grazing has also led to less diversity, loss of rare aquatic plant communities, and a gradually overtaking by terrestrial ecosystems. This change, however, is much slower in the Mediterranean region than in wetter areas, due to the low

Forest fires, an unexpected threat for temporary marshes

In certain regions at risk from forest fires, temporary marshes fed by run-off tend to get filled in by soil erosion when the forest is gone, by intensive scrub clearance and by the development of a network of tracks for fire-fighting[2].

The rapid infilling of the depressions favours colonisation by woody plants and the development of terrestrial habitats.

1 - See n° 6 in the MedWet series
2 - Médail et al., 1996

production of plant biomass during the summer due to drought, and the rapid decomposition of organic matter due to the alternate dry and flooded periods. Grazing by wild and domestic animals provides an impact principally at two levels:

■ Consumption of the vegetation

The direct impact of domestic herbivores on submerged plants is small, but is much stronger on amphibious species, the helophytes and the woody plants, which can considerably limit the development of submerged plants. Food preferences of domestic herbivores vary widely depending on the species. Cattle are less selective. They can feed on twigs of trees and bushes, grasses and a wide range of herbaceous plants; they do not leave patches of ungrazed vegetation. Horses prefer grasses, but can have an important impact on trees, by stripping the bark in winter. Sheep select herbaceous plants and goats woody plants.

The quantitative impact of herbivores on the aquatic vegetation is likely to depend on the animal species, the breed, the plant community and the season, but there is little hard information on these questions.

■ Trampling

The impact of trampling on the soil and vegetation depends on the pressure of the animals and on the soil structure. The pressure depends on the ratio of the weight of the animal to the surface area of the hoof: the pressure is high with cattle, medium with horses, low with sheep and goats. The cohesion of the sediment is greater when it is dry, and low in organic matter. The repeated passage of cattle on flooded ground can be very damaging, particularly if it is rich in organic matter and not very cohesive (sandy, etc.)

	Cattle	Horses	Goats	Sheep
Grasses	+	+	-	+
Rushes	+	+	+	-
Other plants	+	-	+	+
Buds, stems, leaves	-	-	+	-

+: Principal food, -: secondary food

Food preferences of domestic herbivores. After Gordon *et al.*, 1990.

Assets for conservation

The natural context

Temporary marshes have particular characteristics which favour their conservation and enable them to escape certain threats better than other types of wetland:

- The water supply, principally from rainfall, allows a certain number of marshes to be relatively independent from the increasing depletion of the water table by pumping for agricultural, industrial or urban needs.
- Their relatively small watershed excludes them, to some extent, from the effects of pollution from distant sources, which affect the wider hydrological network of larger marshes.
- Their low capacity to store water, which results from the seasonality of these habitats and their small area (this is particularly true of pools), means that temporary marshes are not usually selected as sites for reservoirs for drinking water, irrigation or for the regulation of floods, at least in the Mediterranean region.
- The salinity of coastal marshes reduces the possibility of these sites being used for agriculture, although this problem can be overcome by growing certain crops (e.g. crops requiring alternating flooded and dry periods).

B. Pambour

Temporary marshes have often been levelled and converted to agriculture.

- The small area of certain pools can facilitate their acquisition for conservation objectives. These measures are effective if they take into account the relations between sites vital for the conservation of metapopulations.

The legal context

The importance of temporary marshes is today recognised in several legal texts. In most Mediterranean countries lists of threatened and/or protected species have been established on a regional or a national basis; these include plants of temporary marshes.

For the countries within the European Union, the Appendix 1 of the Habitats Directive provides a list of remarkable habitats in which Mediterranean pools and temporary marshes are grouped into three categories:

- Oligotrophic, with low mineral content in the water, from sandy plains of the west Mediterranean (Code CORINE 22.11 X 22.34)
- Mediterranean temporary marshes (code CORINE 22.34)
- Calcareous oligo-mesotrophic with *Characeae* (code CORINE 22.12 X 22.44)

The conservation value of the flora and the plant communities of Mediterranean temporary marshes is therefore established, and constitutes an asset in favour of the conservation of these habitats within the European network of protected areas, Natura 2000.

Conservation value of temporary pools in France

A recent analysis[1] shows that the temporary, oligotrophic pools in Mediterranean France hold 20 plant associations listed in the Habitats Directive.

The temporary pools are also outstanding for the number of important species they contain. In the Plaine des Maures, which contains 45 protected species on the national and regional levels, 26 are linked to pools and temporary streams. The temporary marshes of the Camargue hold 2 of 12 nationally protected species within this area and 5 of 28 regionally protected.

This recognition of conservation values is unevenly spread geographically. In certain regions like the Massif de l'Estérel, no fewer than 7 plant associations of the Habitats Directive are found, whereas other areas have only one or two. The situation is the same for the diversity of species. A site like the granite plateau of Tre Padule Suartone (Corsica) alone holds 60 % of the rare plants of temporary pools in France.

1 - Médail et al., 1996

Conservation strategies

Once their biological value has been recognised and the threats identified, the conservation of temporary marshes requires the establishment of a strategy which is as wide ranging as possible.

B. Pambour

Management for hunting often converts temporary marshes to permanent ones.

Several issues need to be resolved: how can a network of protected sites be established ? Is the management of these sites for the conservation of the flora compatible with the conservation of the fauna ? Does man always have to intervene ? If so, to what degree ? Two principal, complementary aspects must be considered with respect to the conservation of the flora: habitat and species conservation. Each of them can be practised with different degrees of intervention[1].

Habitat conservation

In undisturbed temporary marshes, it must be emphasised that intervention involving the factors which ensure the perennity of the ecosystem (water regime, grazing), and which contribute to maintaining species richness, should be reduced to an absolute minimum. These habitats are particularly sensitive to any change in the existing management, whether the abandonment of old forms of management or the introduction of new ones.

■ The loss of certain practices

Making a site into a nature reserve often results in the loss of traditional agricultural practices (especially grazing) which maintained the habitat and prevented succession into a terrestrial system. Paradoxically, without active management, the temporary marshes and their rare species may disappear from protected sites for this sort of reason. Protection should include the maintenance or the re-establishment of certain activities, so long as they are adapted to the conservation objectives; a written management plan is often necessary to ensure this.

■ Compatibility between different management objectives

In the important coastal, temporary marshes, the conservation or management objectives very often focus on waterbirds (especially for hunting) or pastoralism. The conservation of other animal groups (fish, invertebrates) or plants is secondary, and generally happens only by chance. Management directed towards waterbirds or domestic mammals tends to limit the summer hydrological stress and maintain the plant production. This type of management will not only reduce the habitat's species diversity, but also the originality of the communities, which are replaced by more commonplace ones.

1 - Falk, 1990

B. Pambour

Some temporary marsh species can survive in ricefields despite intensive farming techniques (eg. *Zannichellia, Chara, Triops*).

This pattern is clearly seen in the Camargue. And yet livestock production, the conservation of waterbirds, or hunting are not necessarily incompatible with the conservation of floristic richness.

When management is necessary, strategies combining several objectives can be applied:

- At the site level: the conservation of the floristic richness of temporary marshes demands a dry period of a certain minimum length. This is compatible with the constitution of a submerged plant community for waterbirds in the winter if the summer flooding is partial and sufficiently early. If a water regime is applied to favour the dominance of helophytes, grazing during the summer period can limit their development in favour of submerged plants. Management with several objectives, therefore, implies the control of many management tools. The creation of little pools is possible, and is neither difficult nor expensive.

- At the regional level: the general objective will, in this case, be to try and recreate the spatial and temporal variability of the Mediterranean temporary marshes. For this, the water management could vary not only within sites from year to year, but from one site to another within the same region. This strategy, especially adapted to the conservation of floristic richness, is compatible with the management of waterbirds because it allows a sufficient number of marshes to be flooded at different seasons for breeding, migrating and overwintering birds. The movement of birds within a network of marshes that assures several different functions, can only improve the exchanges between isolated plant populations.

■ Extending conservation efforts across an area

The conservation of temporary marshes can be done using two different strategies: to protect a large number of small sites or a small number of large sites. This much discussed problem can be approached from different angles: species richness of communities, the abundance of certain populations, rarity or vulnerability of species, etc. The conservation of biodiversity involves knowing whether total richness is greater and better protected in one site, or in several sites of the same area. This information is not yet available for temporary pools. In the long term, a network of small sites poses a number of problems:

- a risk of extinction of small isolated populations: this is less in temporary marshes where the flora is dominated by annual species (aquatic, amphibious or terrestrial), by the large stocks of seeds in the ground.

- a risk of loss of genetic diversity: with hence insufficient gene-flow within a small population, the ability of the seeds to germinate and the reproductive success can be reduced. These effects would threaten the future of the annual plants of temporary marshes which need to reconstitute their seed banks.

The conservation of small sites is therefore possible if the distance allows exchanges of individuals or propagules between them. The nature reserve of Roquehaute (Hérault, France) protects a large number of temporary pools on 158 ha, each only a few tenths of a hectare in size, thus creating an "archipelago" isolated in the maquis.

Two essential tools for the management of temporary marshes

■ Water management, the top priority...

The alternation of dry and wet periods is the key to the conservation value of temporary marshes. If it still occurs, this alternation must be conserved. If the flooding regime has not been disturbed, it is essential not to intervene and not to modify it. When, however, the water regime is controlled by man, the management objectives must be defined, because the dates and length of flooding determine the type of plant community.

Water management is critical.
Too much can be as bad as too little.

■ ...then grazing

The use of animals as management tools implies that the varied and complex effects of grazing on the vegetation are well-known. The large herbivores commonly raised are all generalist feeders which eat hundreds of different plant species, but they are often very selective (choosing particular plants at a given time). The effects of their grazing, trampling and more or less localised deposits of urine and faeces, affect the plants differently, according to their growth stage.

Goats and sheep feed exclusively on dry ground and are useful only for controlling vegetation during the dry period. Horses and cows can feed in water, relatively deep, depending on the breed. The lighter in weight they are, the better it is for the water-logged ground. The Camargue cattle and horses are very efficient at limiting emergent vegetation in marshes because they go readily into water to eat their preferred species (in particular reeds, but also *Scirpus maritimus*).

From a conservation point of view, the use of grazing should take into account the natural plant dynamics and the other management objectives of the site. A judicious choice of species(s), breed(s), grazing pressure and grazing periods can allow for effective control of the vegetation in temporary marshes at low cost, and can even make plant management economically viable.

Conservation and management

Conservation of species

The conservation of species in their habitat is always preferable to that of species ex situ. However, it is not always possible, and different degrees of intervention can be distinguished.

■ The reinforcement of populations

This can be achieved by planting individuals in sites occupied by a species, or else in favourable sites. The objective is to build up the numbers to ensure the survival of the population, and is best done with individuals from the same population or one nearby, which have been cultivated. The ecological and biological requirements of the population must be well-known, and the cultivation techniques need to be mastered. The individuals are then re-introduced, usually as young plants. These techniques are used for very threatened, long-lived species and could be applied only to a limited number of species in temporary marshes.

■ Seed banks

Populations of species which are vulnerable can also be stocked in seed banks in specialised centres (gardens and botanical conservatories). The stock of seeds initially produced in the wild can be multiplied artificially, in order to increase the number of seeds which can later be used for repopulating an area. Only a small part of the genetic diversity of populations can be thus conserved, and there is a strong risk of genetic drift.

The work of a botanical conservatory

The National Mediterranean Botanical Conservatory in Porquerolles (France) works at several levels for the conservation of the flora and the vegetation of Mediterranean temporary marshes (its brief allows it to cover three French Mediterranean regions, but not the Alps). Seeds of plants growing in these habitats (e.g. *Cressa cretica, Damasonium polyspermum)* are stocked, and some are grown in nurseries (e.g. *Cressa cretica).* Some populations are reinforced, and new ones are created by planting individuals in suitable habitats (e.g. *Marsilea strigosa*).

The Conservatory contributes to the conservation of habitats by surveying the temporary marshes of the south of France, locating and mapping stations of certain rare plants *(Pilularia minuta)*, raising the awareness of managers, providing technical assistance for the management and the restoration of temporary pools (clearing out of the rock pools of the Colle du Rouet) and advising on the acquisition of marshes by conservation organisations (e.g. the site of *Teucrium aristatum* in the Crau).


P. Grillas

Conclusion

The flora and fauna of temporary marshes are less well-known today than those of other types of wetlands. A conservation strategy for these habitats is urgently needed because they are disappearing rapidly and often imperceptibly. Several issues need attention.

Surveying of temporary marshes

This can be based on a number of existing surveys of Mediterranean wetlands[1]. Mapping can be useful in order to create a network of sites to protect, and particular attention needs to be paid to the links necessary for the maintenance of certain populations, through the exchange of individuals, genes, etc. between sites. A complete inventory of small, dispersed, temporary pools would, however, be very difficult to carry out.

Temporary marshes on a rock substrate, Plaine des Maures, France.

1 - Hecker & Tomas Vives, 1996

A review of knowledge of temporary marshes

A review of the literature on temporary marshes is an important step: it would provide a better understanding of their functioning, stimulate exchange of information and management experience, and allow little known floristic and faunistic groups to be identified for further scientific research, along with other important ecological questions.

Temporary marshes can be used for research in three principal areas: the structure and functioning of populations and aquatic communities, the process of colonisation of habitats and the dynamics of the ecosystems, and finally the physiological adaptations of organisms to variable ecological conditions.

Evaluate the conservation value of temporary marshes

In many Mediterranean countries, not enough is currently known about these habitats to allow their conservation value to be assessed accurately. Work on the botanical and faunistic richness of the sites, and on the abundance of certain populations, endemic or very localised, which they hold, still remains to be done. It is still difficult to rank the conservation value of temporary marshes around the Mediterranean.

Ranunculus revelieri
is protected in France.

J. Roché

Children can benefit greatly from studying the aquatic environment.

Diversify conservation strategies

For temporary marshes to be conserved, many different actions are required. The set of appropriate measures which need to be taken, strategies to be defined, and conservation and restoration techniques to be employed, depends largely on the context of each State. In the west Mediterranean, the European directives already provide a strong framework for this work. In the east of the region, however, other policies need to be conceived and developed.

Training and teaching

The astonishing life cycles of species living in temporary marshes provide an excellent outdoor tool to raise the awareness of the public about the conservation of these habitats. As a first step it will be necessary to convince, and then to train, the people responsible for environmental education.

Glossary

Akene : indehiscent dry fruit.

Angiosperm : higher flowering plants characterised by the protection of ovules within the ovaries of the flower.

Autotroph : an organism capable of synthesising organic constituents directly from inorganic molecules. Green plants containing chlorophyll are autotrophs : they use light energy to assimilate inorganic carbon which serves as primary material for the metabolism.

Biennal : plant with a life cycle covering two successive years.

Cuticle : a non cellular covering produced by the epidermis. In plants, the cuticle is made of waterproof cutin.

Denitrification : the breakdown of nitrates by soil bacteria resulting in the release of gaseous nitrogen.

Dicotyledon : a group of higher plants characterised by an embryo with two cotyledons (monocotyledons, such as grasses, have only one).

Endorheic : a water body having no outflow.

Eutrophication : enrichment of a water body through inflows of nitrates and phosphates or organic material.

Gamete : a sexual cell which will combine with a gamete of the opposite sex.

Halophyte : a plant which grows in soil or water containing a high concentration of salt.

Helophyte : an upright rooted plant whose flowers and leaves are essentially aerial, and whose perennial parts lie in mud.

Hydromorphic : soils of small particle size which contain excess water.

Karst : limestone formation where solution channels have formed tunnels, caverns and depressions.

Metapopulation : a regional population whose stability depends on the exchange of individuals or genes between isolated sites.

Oligotrophic : waterbodies which are poor in plant nutrients.

Osmotic pressure : the pressure that develops when a pure solvent is separated from a solution by a membrane which allows only solvent molecules to pass through it.

Palisade parenchyma : tissue situated on the upper face of the leaves and rich in chloroplasts containing chlorophyll.

Perennial : a plant living longer than one year.

Propagule : an organ of dissemination.

Pteridophytes : branch of the plant kingdom including ferns (Filicales), club mosses (Lycopodiales) and horsetails (Equisetales).

Spongy parenchyma : undifferentiated tissue consisting of large irregular cells with large intercellular spaces.

Tegument : outer envelope of an organ.

Ubiquitous : a term describing species which occur in many different habitats.

Bibliography

Allan, D.G., Seaman M.T., & B. Kaletja - The endorheic pans of South Africa, in "Wetlands of South Africa", Cowan, G.I. (Ed), 75-101, Department of Environmental Affairs and Tourism, Pretoria, South Africa, 1995.

Aubert, G. & R. Loisel - Contribution à l'étude des groupements des *Isoeto-Nanojuncetea* et des *Helianthemetea annua* dans le sud-est méditerranéen français. Annales de l'Université de Provence, vol. 45, 103-241, 1971.

Barbero, M., Giudicelli, J., Loisel, R., Quezel, P. & E. Terzian - Etude des biocénoses des mares et des ruisseaux temporaires à éphémérophytes dominants en région méditerranéenne française. Bulletin d'Ecologie, vol. 13, 387-400, 1982.

Barko, J.W. & R.M. Smart - Comparative influences of light and temperature on the growth and the metabolism of selected submerged freshwater macrophytes. Ecological Monographs, vol. 51, 219-235, 1981.

Bonis, A. - Dynamique des communautés et mécanismes de coexistence des populations de macrophytes immergées en marais temporaires. Thèse de l'Université de Montpellier II, 1993.

Bonis, A. & J. Lepart - Vertical structure of seed banks and the impact of the depth of burial on recruitment in two temporary marshes. Vegetatio, vol. 112, 127-139, 1994.

Bonis, A., Lepart, J. & P. Grillas - Seed bank dynamics and coexistence of annual macrophytes in a temporary and variable habitat. Oikos, vol. 74, 81-92, 1995.

Boutin, C., Lesne, L. & A. Thiéry - Ecologie et typologie de quelques mares temporaires à *Isoetes* d'une région aride du Maroc occidental. Ecologia Mediterranea, vol. VIII (3), 31-56, 1982.

Brock, M.A. & D.L. Britton - The role of seed banks in the revegetation of Australian temporary wetlands, in "Restoration of temperate wetlands", Wheeler, B.D., Shaw, S.C., Fojt, W. and R.A. Robertson (Eds), Wiley and Sons Ltd, 183-188, 1995.

Brtèk J. & A. Thiery - The geographic distribution of the European Branchiopods *(Anostraca, Notostraca, Spinicaudata and Laevicaudata)*. Hydrobiologia, 298, 263-280, 1995.

Carlquist, S. - Island biogeography. Columbia University Press, New York, USA, 1974.

Cody, M.L. & J.McC. Overton - Short term evolution of reduced dispersal in island plant populations. Journal of Ecology, vol. 84, 53-61, 1996.

Corona, M.G. - Antecedentes ecologicos de los humedales de la Provincia de Cadiz. "Plan rector de uso y gestion de las reservas naturales de las lagunas de Cadiz". Junta de Andalucia, 13-24, 1991.

Crawford, R.M.M. - Studies in plant survival. Studies in Ecology, Blackwell Scientific Publications, vol. 11, 1989.

Darwin, C. - On the origin of species. Murray, London, U.K., 1859.

Bibliography

Duarte, C., Montes, C., Augusti, S., Martino, P., Bernues, M. & J. Kalff - Biomasa de macrofitos acuaticos en la marisma del Parque Nacional de Doñana (SW Espana) : importancia y factores ambientales que controlan su distribucion. Limnetica, vol. 6, 1-11, 1990.

Dupuis, P. - Dynamique et production primaire des macrophytes et microphytes des mares temporaires des Jbilets (dayas de la région de Marrakech-Maroc). Thèse de l'Université de Paris VI, 1988.

El Khiati, N. - Les characées (macroalgues) du Maroc : biotypologie des eaux continentales et production dans les dayas. Thèse de l'Université de Aix-Marseille I., 1987.

Ellner, S. & A. Shmida - Why are adaptations for long-range seed dispersal rare in desert plants? Oecologia vol. 51, 133-144, 1981.

Ellstrand, N.C. & D.R. Elam - Population genetic consequences of small population size : Implications for plant conservation. Annual Review Ecology and Systematics, vol. 24, 217-242, 1993.

Falk, D.A. - The theory of integrated conservation strategies for biological diversity in "Ecosystem Management : rare species and significant habitats" R.S. Mitchell, C.J. Sheviak & D.J. Leopold (Eds), New York State Museum Bulletin, vol. 471, 5-10, 1990.

Griggs, F.T. & S.K. Jain - Conservation of vernal pool plants in California, II. Population biology of a rare and unique grass genus *Orcuttia*. Biological Conservation, vol. 27, 171-193, 1983.

Gordon, I.J., Duncan, P., Grillas, P. & T. Lecomte - The use of domestic herbivores in the conservation of the biological richness of European wetlands. Bulletin d'Ecologie, 21: 49-60, 1990.

Grillas, P. - Distribution of submerged macrophytes in the Camargue in relation to environmental factors. Journal of Vegetation Science, vol. 1, 393-402, 1990.

Grillas, P. - Les communautés de macrophytes submergées des marais temporaires oligo-halins de Camargue. Etude expérimentale des causes de la distribution des espèces. Thèse de doctorat de l'Université de Rennes I, 1992.

Grillas, P. & G., Battedou - Effects of flooding date on the biomass, species composition and seed production in submerged macrophyte beds in temporary marshes in the Camargue (S. France). "Wetlands for the Future" Proceedings A.J. McComb (Ed), in press.

Grillas, P., Garcia-Murillo, P., Geertz-Hansen, O., Marba, N., Montes, C., Duarte, C.M., Tan Ham, L. & A. Grossmann - Submerged macrophyte seed bank in a Mediterranean temporary marsh : Abundance and correlation with established vegetation. Oecologia, vol. 94, 1-6, 1993.

Grillas, P., Van Wijck, C. & A. Bonis - The effect of salinity on the dominance-diversity of coastal experimental communities of coastal submerged macrophytes. Journal of Vegetation Science, vol. 4, 453-460, 1993.

Grillas, P., Van Wijck, C. & A. Bonis - Life history traits : a possible cause for the higher frequency of occurence of *Zannichellia pedunculata* (Reichenb.) than of *Zannichellia obtusifolia* (Talavera, Garcia Murillo & Smit) in temporary marshes. Aquatic Botany, vol. 42, 1-13, 1991.

Grime, J.P. - Competitive exclusion in herbaceous vegetation. Nature 242, 344-347, 1973.

Guerlesquin, M., & V. Podlejski - Characées et végétaux submergés flottants associés dans quelques milieux camarguais. Naturalia Monspeliensia, série Botanique, 36, 1-20, 1980.

Hafner, H., - Contribution à l'étude écologique de quatre espèces de hérons *(Egretta g. garzetta L., Ardeola r. ralloides Scop., Ardeola i. ibis L., Nycticorax n. nycticorax L.)* pendant leur nidification en Camargue. Thèse de l'Université de Toulouse, 1977.

Hecker, N., & P., Tomas Vives (Eds) - The status of wetland inventories in the Mediterranean region. MEDWET/IWRB Publication n° 38, 146 p., 1996

Hili, C., Axiak, V. & P.J. Schembri - The Ghadira reserve : physico-chemical characteristics of the pool. Centro, 1 (5), 5-11, 1990.

Keeley, J.E. & D.R. Sandquist - Carbon : freshwater plants. Plant, Cell and Environment, vol. 15, 1021-1035, 1992.

Kirk, J.T.O. - Light and photosynthesis in aquatic ecosystems. Cambridge University Press, 401 p., 1986

Lanfranco, E. - The vegetation of the Ghadira nature reserve. Centro 1 (5), 1-4, 1990.

Médail, F., Michaud, H., Molina, J. & R. Loisel - Biodiversité et Conservation des phytocénoses des mares temporaires dulçaquicoles et oligotrophes de France méditerranéenne. Actes des 7e Rencontres de l'ARPE, Colloque scientifique international BIO'MES, Digne, 47-57, 1996.

Nöllert, A. & C. Nöllert - Die Amphibien Europas Bestimmung - Gefährdung-Schutz Franckh- Kosmos Verlag, Stuttgart, 1992.

Poizat, G. & A.J. Crivelli - Use of seasonally-flooded marshes by fish in a Mediterranean wetland : timing and demographic consequences. Journal of Fish Biology, vol. 51, 106-119, 1997 .

Pont, D., Crivelli, A.J. & F. Guillot - The impact of three-spined sticklebacks on the zooplankton of a previous fish-free pool. Freshwater Biology, vol. 26, 149-163, 1991.

Pottier-Alapetite, G. - Note préliminaire sur l'*Isoetion* tunisien. Bulletin de la Société Botanique de France, vol. 99 (10), 4-6, 1952.

Ramdani, M. - Ecologie des crustacés (copépodes, cladocères et ostracodes) des dayas marocaines. Thèse de l'Université d'Aix-Marseille, 1986.

Redbo-Torstensson, P. & A. Telenius - Primary and secondary seed dispersal by wind and water in *Spergularia salina*. Ecography, vol. 18, 230-237, 1995.

Rita, J. & G. Bibiloni - Zonation de la vegetacion hidrofila de balsas periodicas en las zonas semiaridas de Baleares. Orsis, vol. 6, 61-74, 1991.

Ritland, K. - The joint evolution of seed dormancy and flowering time in annual plants living in variable environments. Theoretical Population Biology, vol. 24, 213-243, 1983.

Ritland, K. & S. Jain - The comparative life-histories of two annual *Limnanthes* species in a temporally variable environment. The American Naturalist, vol. 124, 656-679, 1984.

Synge, H., (ed) - The biological aspects of rare plant conservation. Wiley & Sons, Chichester, 1981.

Tamisier, A. - Le régime alimentaire des sarcelles d'hiver *Anas crecca L.* en Camargue. Alauda 19, 4, 1-311, 1971.

Tamisier, A. & P. Grillas - A review of habitat changes in the Camargue. An assessment of the effects of the loss of biological diversity on the wintering waterfowl community. Biological Conservation, vol. 70, 39-47, 1994.

Terzian, E. - Ecologie des mares temporaires de l'*Isoetion* sur la Crau et l'Esterel (France). Thèse de l'Université de Marseille, 1979.

Todd, D.K. - Groundwater hydrology.2d edition, Wiley and Sons, New York. 1980.

Van der Pijl, L. - Principles of dispersal in higher plants. Springer Verlag, Berlin, Germany, 1982.

Van Vierssen, W. - The ecology of communities dominated by *Zannichellia* taxa in Western Europe. I. Characterization and autecology of *Zannichellia* taxa. Aquatic Botany, vol. 12, 103-155, 1982.

Verhoeven, J.T.A. - The ecology of *Ruppia*-dominated communities in western Europe. I. Distribution of *Ruppia* representatives in relation to their autecology. Aquatic Botany, vol. 6, 197-268, 1979.

Verhoeven, J.T.A. & W. Van Vierssen - Structure of macrophytes dominated communities in two brackish lagoons on the island of Corsica, France. Aquatic Botany, vol. 5, 77-86, 1978.

Verhoeven, J.T.A., Jacobs, R.P.W.M. & W. Van Vierssen - Life strategies of aquatic plants : some critical notes and recommendations for further research, in : "Studies on aquatic vascular plants", Symoens, J.J., Hooper, S.S. and P. Compère (eds), Royal Botanical Society of Belgium, Brussels, Belgium, 158-164, 1982.

Vivian-Smith, G. & E.W. Stiles - Dispersal of salt marsh seeds on the feet and feathers of waterfowl. Wetlands, vol. 14 (4), 316-319, 1994.

Wiggins, G.B., MacKay, R.J., & I.A. Smith - Evolutionary and ecological strategies of animals in temporary pools. Archiv for hydrobiology, Suppl. 58, 97-206, 1980.

Volder, A., Bonis, A. & P. Grillas - Comparative effects of flooding and drought on the reproduction of an amphibious plant *Ranunculus peltatus*. Aquatic Botany, in press.

Zedler, P.H. - Life histories of vernal pool vascular plants. In "Vernal pool plants-their habitat and biology", Ikeda D.H. and R.A. Schlising (eds), Studies from the Herbarium n°8, California State University, Chico, USA, 123-146, 1990.

Zedler, P.H. - The ecology of southern California vernal pools : a community profile. U.S. Fish & Wildlife Service Biological Report 85 (7.11), 1987.

Zedler, P.H. & C. Black - Seed dispersal by a generalized herbivore : rabbits as dispersal vectors in a semiarid California vernal pool landscape. American Midland Naturalist, vol 128, 1-10, 1992.

Zedler, P.H., Frazier, C.R. & C. Black - Habitat creation as a strategy in ecosystem preservation : an example from vernal pools in San Diego County in : "Interface between ecology and land development in California", J.E. Keeley (ed), Southern California Academy of Sciences, Los Angeles, USA, 239-247, 1993.

Index

The **Station biologique de la Tour du Valat** was established in the Camargue (France) in 1954 by Dr. Luc Hoffmann as a private research institute, primarily for field ornithological studies.

In 1993 the estate consists of 2500 ha of land belonging to the Fondation Sansouire, created under French law in 1976. The estate is one of the few in the eastern Camargue on which extensive areas of near-natural landscapes have survived the post-war expansion of arable agriculture. Funding for the research and conservation programme of the Station comes from a variety of national and international organisations, but the major part of the core funding is provided by the Fondation Tour du Valat, a foundation under Swiss law.

The scientific programme of the station has evolved over the years, and has included programmes on the management of vegetation using domestic herbivores, fish ecology, optimal foraging strategies, behavioural studies, and migration and breeding success of colonial waterbirds. Most of these studies have been undertaken in the Camargue, but the Station has increasingly worked in collaboration with other scientists in the Mediterranean region.

This programme has provided the Station with a fundamental understanding of Mediterranean wetland ecology which can be applied to wetland management problems in the region.

Published with the financial support of the Commission of the European Communities

ISBN : 2-910368-16-5

FF 5