Contribution to the coastal bryophytes of the Northern Mediterranean: Are there halophytes among bryophytes?

Marko Sabovljević & Aneta Sabovljević

Institute of Botany and Botanical Garden, Faculty of Biology, University of Belgrade, Takovska 43, 11000 Belgrade, Serbia, marko@bfbot.bg.ac.yu

Received: April 07, 2007 ▷ Accepted: April 11, 2007

Dedicated to the memory of Prof. Dr Radomir Konjević (1946–2006)

Abstract. A first approach to investigation of halophytism among bryophytes has been made. Extensive bryophyte sampling along the Northern Mediterranean coast was conducted, so as to collect data which bryophytes tolerate salt stress and are exclusive for salt-infulenced habitas, as well as to list bryophytes to be used in further investigations into the phenomena of halophytism wıthin bryophytes.

Key words: bryophytes, halophytism, Northern Mediterranean

Introduction

Halophytes are plants which tolerate or even demand increased sodium chloride concentrations in the water they absorb. Depending on the habitat conditions, they have developed different strategies to survive, sometimes under very high salt content. In accordance with their tolerance and demands for sodium salts, obligate and facultative halophytes are distinguished. The obligate do need some salt; the facultative can also live under freshwater conditions. The obligates are also called true halophytes and thrive when the water contains over 0.5 % (1.0 %) NaCl (Ungar 1978). A small number of plant lineages have developed structural, phenological, physiological, and biochemical mechanisms for salt resistance and true halophytes have convergently evolved in numerous related families (Ungar 1987).

One distinguishes succulent halophytes, halophytes with salt bladders on the leaf surface, and halophytes which excrete salt with water evaporation, the salt crystals remaining visible on the leaf surface (Iraki & al. 1989). Under lower salinity levels some plants are able to exclude the salt taken up otherwise by the roots.

Many plants fall under several halophyte categories. They all possess genes which allow them to master the respective salinity under which they must operate.

The overall definition of a halophyte may therefore be: plants, which are able to live under elevated salinities in their growth media. The salinity level in which they grow varies from slight, to brackish, to medium, to severe, and to above seawater salinity. The genetic and physiological properties which enable them to cope with the salt concentration are presently subject of intense research (eg. Ostrem & al. 1987; Cushman & al. 1989; Csonka & Hanson 1991; Hurkman 1992).

Saline habitats occur along bodies of saltwater, e.g., coastal salt marshes, inland basins with high-evaporation, saline lakes, and lowlands of dry land and desert topography. The electrolytes sodium (a cation) and chloride (an anion) are extremely toxic to most plants at relatively low soil water concentrations, due to deleterious effects on cellular metabolism and ultrastructure (Pennings & Callaway 1992).

A saline habitat often has a low diversity of plants, sometimes even just one dominant species, because so few species are able to resist salt damage (Larcher 1980).

Bryophytes are members of all ecosystems except the marine. The influence of salt water is belived to be negative for the developement of bryophytes (Hart & al. 1991). However, there are some hepatic taxa growing in South European brakish ponds (eg. *Riella* spp.) and some species with an ecological nishe on the rock cliffs with salt water spray at the Atlantic coast (eg. *Schistidium maritimum*). The latter is growing in a very wet climate, which further decreases the influence of salt water spray.

Material and methods

With aim to study which are the bryophytes that tolerate salt water spray in the Mediterranean northern coast, a number of localities have been visited and extensive collection has been made. The bryophytes were recorded on various substrata and in various situations, but no farther than 10 meters inland of the coastline. The nomenclature follows Sabovljević & Natcheva (2006) for hepatics and Hill & al. (2006) for mosses.

The following 27 sites were chosen for investigation and visited in the period 1999–2006 (Fig. 1):

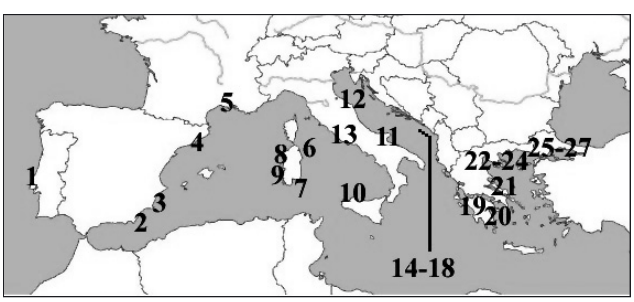

Fig. 1. Recording sites in the Northern Mediterranean: **1.** Portugal, Lisbon surroundings; **2.** Spain, Cabo de Gata; **3.** Spain, La Manga-Mar Menor; **4.** Spain, Barcelona surroundings; **5.** France, Carneaux; **6.** Italy, Sardinia, Olbia surroundings; **7.** Italy, Sardinia, Quartu Sant'Elena; **8.** Italy, Sardinia, Porto Torres; **9.** Italy, Sardinia, Oristano surroundings; **10.** Italy, Sicilia, Palermo surroundings; **11.** Italy, Gargano; **12.** Italy, Monte Conero; **13.** Italy, Circeo National Park; **14.** Montenegro, Jaz; **15.** Montenegro, Kotor surroundings; **16.** Montenegro, Budva surroundings; **17.** Montenegro, Herceg Novi; **18.** Montenegro, Mamula; **19.** Greece, Peloponnese, Kyparissia; **20.** Greece, Peloponnese, Nafplio; **21.** Greece, Evbea; **22.** Greece, Chalkidiki, Kassandra; **23.** Greece, Chalkidiki, Sithonia; **24.** Greece, Thessaloniki surroundings; **25.** Turkey, Trace, Şarköy; **26.** Turkey, Trace, Tekirdağ; **27.** Turkey, Trace, Istanbul surroundings.

Results

Only the species collected more than three times in the studied localities, in different situations, always close to the seaside are presented here (Table 1).

Only 10.52 % of the recorded coastal bryophytes were hepatics. Pottiaceae (60.52 %) was the dominant group of the mosses (89.48 %). Only 7.89 % were pleurocarpous mosses.

Table 1. List of coastal bryophyte species in the Northern Mediterranean. For reference numbers see the legend under Fig. 1.

No.	Species	Site
Liverworts		
1.	*Cephaloziella baumgartneri* Schiffn.	8, 10-13, 19, 20, 23
2.	*Gongylanthus ericetorum* (Raddi) Nees	11, 12, 23
3.	*Pellia endiviifolia* (Dicks.) Dumort.	All
4.	*Southbya tophacea* (Spruce) Spruce	6-12, 15, 19, 22
Mosses		
5.	*Aloina aloides* (Koch ex Schultz) Kindb.	All
6.	*Aloina ambigua* (Bruch & Schimp.) Limpr.	All
7.	*Barbula convoluta* Hedw.	All
8.	*Barbula unguiculata* Hedw.	All
9.	*Bryum argenteum* Hedw.	All
10.	*Bryum capillare* compl.	All
11.	*Ceratodon purpureus* (Hedw.) Brid.	All
12.	*Dicranella howei* Renauld & Cardot	all except 1, 2, 4, 18, 25
13.	*Didymodon acutus* (Brid.) K. Saito	all except 1, 25
14.	*Didymodon fallax* (Hedw.) R.H. Zander	All
15.	*Didymodon insulanus* (De Not.) M.O. Hill	All
16.	*Didymodon luridus* Hornsch.	All
17.	*Didymodon sicculus* M.J. Cano, Ros, Garcia-Zamora & J. Guerra	2, 3, 4, 11, 12, 14, 18, 20, 21, 26
18.	*Didymodon vinealis* (Brid.) R.H. Zander	All
19.	*Eucladium verticillatum* (With.) Bruch & Schimp.	All
20.	*Gymnostomum calcareum* Nees & Hornsch.	All
21.	*Homalothecium aureum* (Spruce) H. Rob.	2, 10, 17, 24, 27
22.	*Hypnum cupressiforme* compl.	All
23.	*Pleurochaete squarrosa* (Brid.) Lindb.	All
24.	*Pseudocrossidium hornschuchianum* (Schultz) R.H. Zander	All
25.	*Pseudocrossidium revolutum* (Brid.) R.H. Zander	All
26.	*Rhynchostegiella tenella* (Dicks.) Limpr.	1, 5, 7, 8, 9, 16, 19, 23
27.	*Schistidium apocarpum* compl.	All
28.	*Scleropodium tourettii* (Brid.) L.F. Koch	6, 7, 8, 9, 10, 14, 22, 23
29.	*Syntrichia calcicola* J.J. Amann	All
30.	*Tortella nitida* (Lindb.) Broth.	All
31.	*Tortula muralis* Hedw.	All
32.	*Trichostomum brachydontium* Bruch	All
33.	*Trichostomum crispulum* Bruch	All
34.	*Trichostomum triumphans* De Not.	all
35.	*Weissia brachycarpa* (Nees & Hornsch.) Jur.	All
36.	*Weissia condensa* (Voit) Lindb.	All
37.	*Weissia controversa* Hedw.	All
38.	*Weissia longifolia* Mitt.	All

Discussion

Salt resistance is the reaction of an organism to salt stress (Yeo 1983; Nešković & al. 2003). Resistance can involve either salt tolerance or salt avoidance. Salt tolerance involves physiological and biochemical adaptation to maintain protoplasmic viability, as cells accumulate electrolytes. Salt avoidance involves structural and physiological adaptation to minimize salt concentrations of the cells, or physiological exclusion by the root membranes in vascular plants. Among vascular plants, halophytes are often classified as excretives and succulents, while another classification recognizes excluders versus includers (Khan & Weber 2006). Excretives have glandular cells capable of secreting excess salts from the plant organs. Succulents use increase in water content within large vacuoles to minimize salt toxicity. Bryophyte mechanisms of salt tolerance have not been defined and compared so far.

There have been no data so far on the salt effects on bryophytes (Schobert 1977; Yancey & al. 1982; Verslues & al. 2006). It is mostly accepted that bryophytes are absent from salty environments. However, according to some examples, *Enthostodon hungaricus* (Boros) Loeske was recorded along alkali saline marches and *Hennediella heimii* (Hedw.) R.H. Zander on salty banks, etc. Shacklette (1961) reported that some bryophytes form communities in mild saline environments. There are no data whether these species can be considered obligate or facultative halophytes, nor what have been the mechanisms for their survival under such unfavourable conditions.

Ecophysiological aspects allow differentiation between obligate, facultative, and habitat-indifferent halophytes (Cushman 2001; Versleus & al. 2006):

- Obligate halophytes grow only in salty habitats. They show clear optimisation of their development through an increased salt supply during experiments. Many *Chenopodiceae* belong to this category. Among bryophytes, possibly only the hepatics from genus *Riella* can be included into this category, owing to their confinement to brakish ponds close to the seashore, along with the moss *Schistidium maritimum* growing exclusively on rocks sprayed by sea water. However, further investigations are needed in this direction.
- Facultative halophytes are able to get established on salty soils, but their optimum lies in a salt-free or at least low-salt environment. The salt is tolerated. Most *Gramineae*, *Cyperaceae*, and *Junaceae,* as well as a large number of dicotyledons like *Glaux maritima, Plantago maritima, Aster tripodium*, etc., belong to this group. Among bryophytes, *Enthostodon hungaricus* belongs potentially there too. It grows in salty alkaline marshes but on the soil above the marsh level. Another example is *Hennediella heimii,* often present along the salt marshes and motorways, on soils influenced by winter salting.
- Plants which are indifferent to their habitat are still able to cope with salty soils in nature. Nevertheless, they usually do live on salt-free soils. On the one hand, they are able to compete with the salt-sensitive species and, on the other, are able to live on salty soils, too. Examples are *Chenopodium glaucum, Myosurus minimus, Potentilla anserina,* some grass species, etc. In many species, the populations living on salty soils and those on salt-free soils differ genetically. Examples are *Festuca rubra, Agrostis stolonifera and Juncus bufonius*. This group probably includes all bryophyte representatives recorded by us along the North Mediterranean coasts during this study. Due to their low competitive abilities as compared to vascular plants, their advantage is in the period of their functional activity and relationships with the above-growing vascular plants. Many interesting assumptions could be made on this issue, but this will be the aim of further investigations.

Among vascular plants, halophytes are often succulent, many species have salt glands, and others are able to store considerable concentrations of salt within their vacuole. The plants have to cope with a strained water balance, as the uptake of water is accompanied by significant uptake of salt. Proteins of the halophytes, as a rule, are no less sensitive to salt than those of other plants. Different strategies are used to cope with high salt content:

- Succulence. The active concentration of salt in the vacuole and the storage of large volumes of water help keeping low the concentration of salt in the cytoplasm. Some bryophytes like *Aloina* spp., for example, have succulent appearance. Some species are often found in the salt-water influence zone, but the glands and other mechanism of potential salt tolerance are unknown.
- Excretion. The salt is excreted by the salt glands. The salt content of the tissue is low. It is not ob-

vious whether this phenomenon has been present among the bryophytes.

- Halophytes without a regulating mechanism. The classic example of this type is *Juncus gerardii*. Its salt content rises steadily throughout one period of vegetation until reaching a limit that is deadly for the plant. Nevertheless, the time is long enough for the plant to go through a complete cycle of development. To this group belong most of the bryophytes which show some level of salt tolerance, due to inactivity of the life function during the period of drought and extreme salt exposure.
- Root filtering types. Mangroves set an example. The quality of the filtering effect fluctuates largely. Some grasses have very efficient filters, while those of succulents are not very effective. The uptake of sodium depends on the membrane and the efficiency of its ion pumps (increased activity of the molecules and/or increased number of pumps per square unit). Salt-tolerant *Vitis*-species are characterised by a high percentage of phosphatidylcholin in their membranes, the percentage of galactosylglycerin is reduced. It looks, as if these lipids are able to modulate the activity of the pumps. There are no bryophytes in this group since they have no roots. However, the filtering effect of ion pumps is to be investigated among bryophytes found in salty environments.

Halophytes are usually less fit in salt-free habitats than other plants (Pennings & Callaway 1992). This is partly due to their relatively slow development. Among the damages salt causes to plants are the osmotic effects, when uptake of water becomes more difficult.

- Disorganisation of the mineral nutrition, selectivity of the ion uptake is disturbed. The ion balance of the cells is disturbed.
- Toxic effects: salt effects. Precipitation or partial denaturation of proteins, changes in their ability to be regulated, changes in the permeability of membranes, etc.

All these effects occur in bryophytes, but owing to their peculiar biology many others still have to be investigated. For example, since nutrition comes from precipitation, is that an advantage or disadvantage for the organisms living in such a harsh environment? Or, since there is a haplotype genome within bryophytes, how the bryophytes can repair damages caused by salt overexposure. Are these mechanisms more reliable and precise than those in vascular plants?

Conclusion

Bryophytes are non-halophyte. However, it can be assumed that some species can withstand the salt influence. These can be considered in general as facultative halophytes. Among the species recorded under the conditions of sea water impact, not all equally tolerate salt deposition. Conditions of the habitat for some of them are mitigated by the flow of fresh water (eg. *Pellia endiviifolia*) and/or by the dense canopy of vascular plants growing above them. Since 60.52 % of all coast-recorded bryophytes belong to pottioid mosses, it can be assumed that their survival strategy is biological inactivity during most of the year (Zander 1993). The anabiosis is split during wet rainy periods which again lowers salt deposition or spray.

This list gives some initial data on the potentaialy salt-tolerant bryophyte species and/or facultative bryo-halophytes. Further investigations into the biology of these species is expected to provide more valuable data and to answer many still unanswered questions about the physiological and biochemical responce of bryophytes to salt and the mechanisms of those living in salty environment which certainly differ from the mechanisms in vascular plants.

Acknowledgement. The authors are grateful to Dr. Rayna Natcheva (Sofia) and to the unknown reviewer for their valuable comments and remarks on the manuscript.

References

Csonka, L.N. & Hanson, A.D. 1991. Prokaryotic osmoregulation: genetics and physiology. – Annual Rev. Microbiol., **45:** 569-606.

Cushman, J.C. 2001. Osmoregulation in plants: Implications for agriculture. – Amer. Zoologist, **41**(4): 758-769.

Cushman, J.C., Meyer, G., Michalowski, C.B., Schmitt, J.M. & Bohnert, H.J. 1989. Salt stress leads to differential expression of two isogenes of phosphoenolpyruvate carboxylase during Crassulacean acid metabolism induction in the common ice plant. – Plant Cell, **1**(7): 715-725.

Hart, B.T., Bailey, P., Edwards, R., Hortle, K., James, K., McMahon, A., Meredith, C. & Swadling, K. 1991. A review of the salt sensitivity of the Australian freshwater biota. – Hydrobiologia, **210**: 105-144.

Hill, M.O., Bell, N., Bruggemann-Nannenga, M.A., Brugués, M., Cano, M.J., Enroth, J., Flatberg, K.I., Frahm, J.-P., Gallego, M.T., Garilleti, R., Guerra, J., Hedenäs, L., Holyoak, D.T., Hyvönen, J., Ignatov, M.S., Lara, F., Mazimpaka, V., Muñoz, J. and Söderström, L. 2006. An annotated checklist of the mosses of Europe and Macaronesia. – J. Bryol., **28**: 198-267.

Hurkman, W.J. 1992. Effect of salt stress on plant gene expression: A review. – Pl. & Soil, **146**(1-2): 145-151.

Iraki, N.M., Bressan, R.A., Hasegawa, P.M. & Carpita, N.C. 1989. Alteration of the physical and chemical structure of the primary cell wall of growth limited plant cells adapted to osmotic stress. – Plant. Physiol., **91**(1): 39-47.

Khan, M. A. & Weber, D. J. (eds.) 2006. Ecophysiology of High Salinity Tolerant Plants. Springer, Netherlands.

Larcher, W. 1980. Physiological Plant Ecology. Springer Verlag, Berlin.

Nešković, M., Konjević, R. & Ćulafić, Lj. 2003. Plant Physiology. NNK International, Beograd (in Serbian).

Ostrem, J.A., Olson, S.W., Schmitt, J.M. & Bohnert, H.J. 1987. Salt stress increases the level of translatable mRNA for phosphoenolpyruvate carboxylase in *Mesembryanthemum crystallinum*. – Pl. Physiol., **84**(4): 1270-1275.

Pennings, S.C. & Callaway, R M. 1992. Salt marsh plant zonation: The relative importance of competition and physical factors. – Ecology, **73**(2): 681-690.

Sabovljević, M & Natcheva, R. 2006. Checklist of the liverworts and hornworts of Southeastern Europe. – Phytol. Balcan., **12**(2): 169-180.

Schobert, B. 1977. Is there an osmotic regulatory mechanism in algae and higher plants? – J. Theor. Biol., **68**(1): 17-26.

Shacklette, H.T. 1961. Substrate relationships of some bryophyte communities on Latouche Island, Alaska. – Bryologist, **64**(1): 1-16.

Ungar, I.A. 1978. Halophyte seed germination. – Bot. Rev., **44**(2): 233-264.

Ungar, I.A. 1987. Population ecology of halophyte seeds. – Bot. Rev., **53**(3): 301-334.

Verslues, P.E., Agarwal, M., Katiyar-Agarwal. S., Zhu, J. & Zhu, J.-K. 2006. Methods and concepts in quantifying resistance to drought, salt and freezing, abiotic stresses that affect plant water status. – Plant J., **45**(4): 523-530.

Yancey, P.H., Clark, M.E., Hand, S.C., Bowlus, R.D. & Somero, G.N. 1982. Living with water stress: evolution of osmolyte systems. – Science, **217**(4566): 1214-1222.

Yeo, A.R. 1983. Salinity resistance: Physiologies and prices. – Physiol. Pl., **58:** 214-222.

Zander, R. 1993. Genera of the *Pottiaceae*: mosses of harsh environments. – Bull. Buffalo Soc. Nat. Sci., **32**: 1-378.