New ecology and new classification for phytosociology of hydrophilic lichens in acid watercourses in France

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Summary

1. Based on a literature search and the study of 300 samples of saxicolous calcifuge lichen communities obtained with the "total sampling" method along several watercourses in continental France, the authors propose the nomenclature of "ekreophilic" for lichens developing on rocks subjected to prolonged water flows and "hydrophilic" when they colonise supports subjected to periodic immersion by watercourses.

2. Statistical analyses of the 300 samples show the existence of three groups defined by their contact times with water. The authors propose the names "subhydrophilic", "mesohydropilic"

and "hyperhydrophilic" for lichens in the upper part of the minor bed, the lower part of the minor bed and in the low-flow channel, respectively.

3. A new classification for phytosociology, or plant communities, is proposed. It is defined by the existence of one class of hydrophilic lichens, three orders corresponding to the different times of contact with water, six alliances that depend on bioclimatic stage and finally several associations whose flora compositions should be defined by further work. Research perspectives resulting from this new ecological concept, and the role of symbiotic organisms in phanerogam colonisation of land exposed by receding water are discussed.

Introduction

The study of the ecology of lichen communities on siliceous rocks started in 2003 by work in the Tarn Department of France, expanding over the next six years to several other French Departments. The reason behind this work is that few European publications are devoted to this subject and none involve France. Several articles have provided interesting data on the distribution of hydrophilic lichens but only a handful dealt with the general and comparative ecology of varied aquatic lichen communities.

Published data, the methods used for taking and processing samples, as well as the analysis of the results are presented in this note, whose aim is to propose a new ecological conception and a new nomenclature of hydrophilic lichen communities in acid continental aquatic ecosystems. It concludes with research perspectives arising from these new data.

Method

Lichens depend on alternating dry and wet periods, but excessive hydration and permanent desiccation are harmful (Ried, 1960; Dietz and Hartung, 1999). Their symbiosis provides a high after growth capacity and a very broad range of habitats. They can colonise virtually all

supports in all environments: from the banks of watercourses to the most varied terrestrial ecosystems. There are many zones of ecological contacts among ecosystems (James et al., 1977) but the compositions of terrestrial and aquatic flora are very different. Aquatic lichens have an ecological specificity.

There are two groups of aquatic lichens, called ekreophilic when they are on rocks subjected to prolonged water flows, and hydrophilic when they colonise supports subjected to periodic immersion by watercourses (James et al, 1977; Roux et al, 2006).

One factor determining the structure of hydrophilic lichen communities is the duration of immersion by watercourses (Santesson, 1939). Several publications have described a transversal zonation of lichens in watercourse beds (Fig. 1) (or in lakes) with respect to the immersion duration of the species in question (Beschel, 1954; Gilbert, 1996; Gilbert and Giavarini, 1997, 2000; Aptroot and Seaward, 2003). These zonations are based primarily on the European system of the yearly fraction of time during which rocks are immersed vs. their distance from the mid-point of watercourses (Fig 2).

On-site experiments (Keller and Scheidegger, 1994) or specific studies (Valcarcel and Carballal, 2002) have provided quantitative data on the immersion times of river bank rocks colonised by lichens. Three transversal zones have been defined on the basis of annual immersion periods: more than 10 months, between 3 and 10 months and less than 3 months. These results confirm the proposal of Santesson (1939).

The period of immersion is not the only parameter determining hydrophilic communities, since the rate of rock surface drying also plays a non-negligible role (Coste, 2005). In addition, there are so-called riparian "buffer" zones where the lack of immersion is compensated by the excessively shaded location of rocks (Nascimbene et al, 2007) that protects from desiccation, confirming prior results (Coste, 2005).

Hydrophilic lichen communities are impacted by many ecological factors other than the duration of immersion or the rate of desiccation of supports (Perreira, 1992; Krzewicka and Galas, 2006; Thüs and Schultz, 2009). Thus, the structure of hydrophilic lichen communities is determined by the chemical nature of the water, current strength, the type and stability of rocks, the sediment load of the water and temperature (James et al, 1977; Thüs, 2002; Aptroot and Seaward, 2003; Coste, 2005).

There are two basic methods applied to ecology studies, the so-called "classical" method of partial sample gathering (Wirth, 1972) and the total sampling method (Roux, 1990). The first has been and is still used in studies of plant communities, or phytosociology. The second method was recently applied to hydrophilic lichens communities on siliceous rocks in the Tarn Department of France (Coste, 2005). Although this method is rapidly implemented in the field, it requires long and fastidious prior laboratory work. This method provides very precise results on ecology and flora that give rise to interesting hierarchic rankings.

Three hundred samples were taken at varying distances from the centre of watercourses: in the low-flow channel, the lower part of the minor bed and the upper part of the minor bed. These three zones are involved by the above-mentioned annual immersion times of rocks: more than 10 months, between 3 and 10 months and less than 3 months.

Samples were taken in several French Departments (Fig 3) and were analysed using statistical processing software (R software).

Results

The canonical analysis of the results (Fig 4) shows that the localisation of samples with respect to the centre of watercourses determines the structure of lichen communities (Fig 5). The compositions of flora in samples from the three support immersion zones exhibit highly significant differences. An NMDS (non-metric multidimensional scaling) classification also

showed that the flora compositions of the three groups differ as a function of the bioclimatic stage.

Field observations often find communities in the lower part of the minor bed of watercourses that are normally found in the low-flow channel. This illustrates buffer zones where the lack of immersion is compensated by local protection from desiccation of rock surfaces. These features are minimised by the use of statistical tools. Good understanding of species and long field experience are necessary to avoid the ecological consolidation of communities based on features of the terrain.

Conclusions, discussion and perspectives

Examining prior work has led to the differentiation of lichens on rocks subjected to relatively constant water flows and those on rocks undergoing periodic immersion in watercourses, respectively called ekreophilic and hydrophilic groups that can also be called aquatic or amphibious. This older work pointed out the existence of several lichen communities whose structure depends on their duration of immersion. Statistical analyses of the 300 samples taken in the present work have confirmed this assertion and have defined three groups, each specific to a zone of immersion. Even though results of field observations were somewhat minimised by the statistical tool used, they showed the existence of buffer zones. This involves not only the duration of immersion that determines the structure of lichen communities, but also the drying rate of rock surfaces. It is recommended to use the term "duration of contact with water" rather than "duration of immersion". As a result, a new nomenclature of hydrophilic lichen communities should be considered. It is proposed to call lichens in the contact zone of more than 10 months, between 3 and 10 months and less than 3 months "hyper-hydrophilic", "meso-hydrophilic" and "sub-hydrophilic", with some minor

variation related to the existence of buffer zones. Figure 6 summarises the ecological conception of hydrophilic lichen communities.

The structure of each of these groups identified is also determined by climatic conditions related to vegetation stages, making it possible to propose an overall phytosociology profile (figure 7). One group of species is found in all samples regardless of contact times with water. These lichens can be considered as representatives of the phytosociology class of hydrophilic lichens on siliceous rocks. A second group is found only in one of the three immersions zones, and these species can be considered as representatives of the phytosociology order. Finally, each order defined contains specific groups of species per bioclimatic stage and can be considered as representatives of phytosociological alliances. These alliances contain the combination of two or even three species, depending on very strict local ecological characteristics. Only hyper-hydrophilic groups do not involve associations and all samples contained a dispersion of species. In contrast to sub-hydrophilic and meso-hydrophilic groups, this dispersion of species may have two origins: either hyper-hydrophilic associations in France at the limit of the area of distribution, or there are no climactic associations in the low-flow channel. Although hydrophilic lichen associations in France are at the limits of the zone, they probably reach a climactic stage in other regions of Europe, e.g. central Europe. Specific work in these regions should confirm or refute this opinion. A climactic stage is characterised by small heterogeneous ecological niches, high biomass production and a complex and diversified trophic system (Dajoz, 2006). In the low-flow channel, however, ecological niches are large and homogeneous, biomass is low and the food chain is reduced to only fresh water invertebrate. Hyper-hydrophilic associations apparently do not exist and can be considered as "permanent pioneer" groups.

For each phytosociological unit thus defined, the list of all species characteristic of each group thus defined will be the subject of a future publication.

For each group defined, it is also necessary to identify the physiological specificities involved in adaptation to ecological conditions, in particular photosynthesis in aquatic and open air environments, and its role in the food chain and biogeochemical cycles.

The present results will lead to a better understanding of the passage of lichens from aquatic to terrestrial life, and more broadly the comprehension of the role of lichens and symbiotic organisms in general, in the colonisation by higher plants of land exposed by receding waters.

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Gilbert, 1996 ; Gilbert et Giavarini, 1997 ; Aptroot et Seaward - 2003		
Vertical zonation	Nominations	Observations
Upper terrestrial zone	Not affecting by running water	No fresh water lichens
Fluvial xeric zone	Irregularly sprayed or submersed	Two différents zones can usually be discerned
Fluvial mesic zone	Immediately above the submersed zone	Characterized by foliose lichens
Submerged zone	Inunded for the most of the year	Fresh water species of the genius *Verrucaria*

Fig. 1 : Zonation according to Gilbert (1996) and Gilbert and Giavarini (1997), used by Aptroot and Seaward (2003).

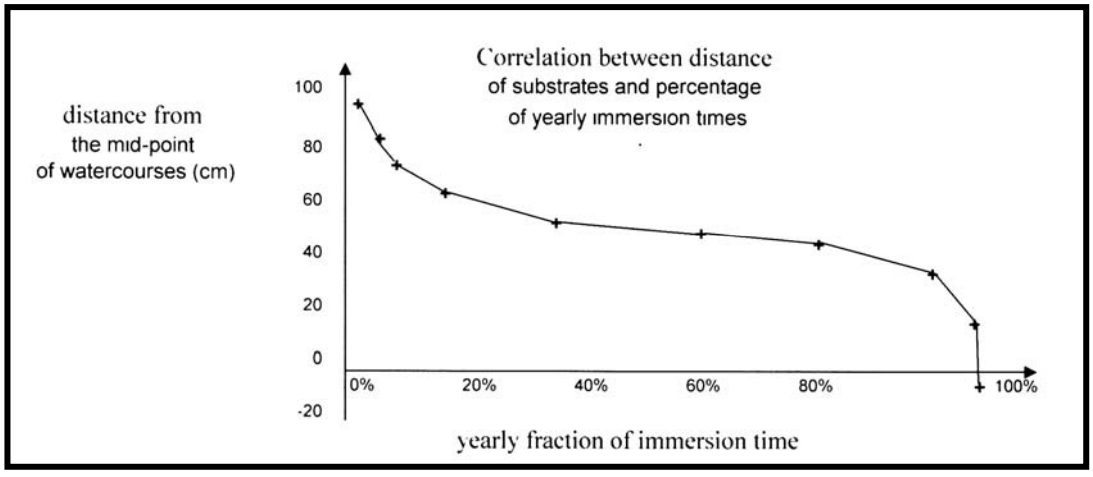

Fig. 2 : Correlation between distance of substrates and percentage of yearly immersion times. (European system, Santesson, 1939).

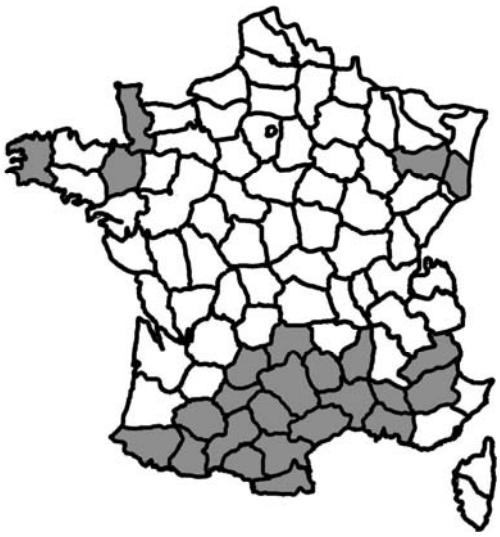

Fig. 3 : Sampling sites in France.

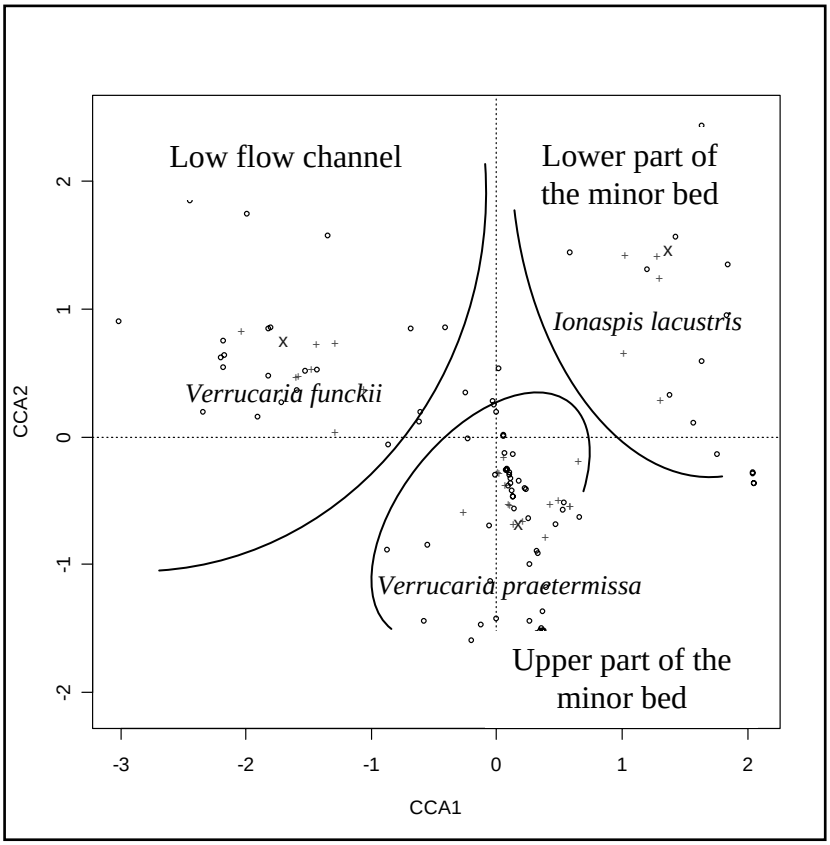

Fig. 4 : Results of the canonical analysis of 300 samples

(CCA général $P < 0.005$ et factors $P < 0.002$).

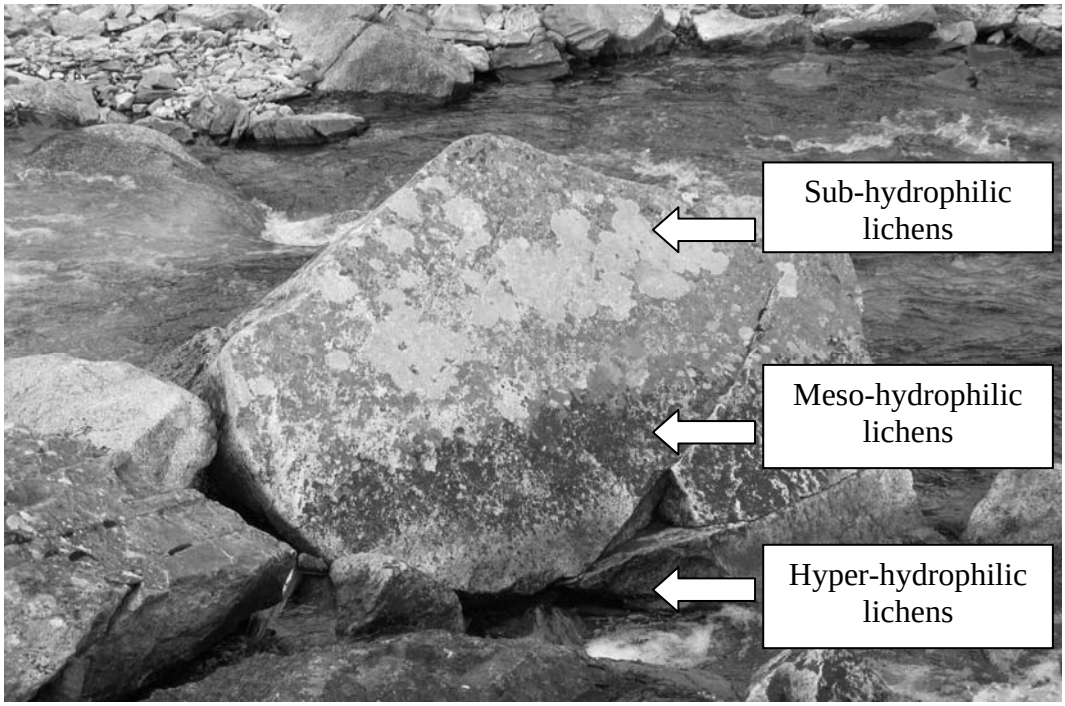

Fig. 5 : Example of hydrophilic lichen communities.

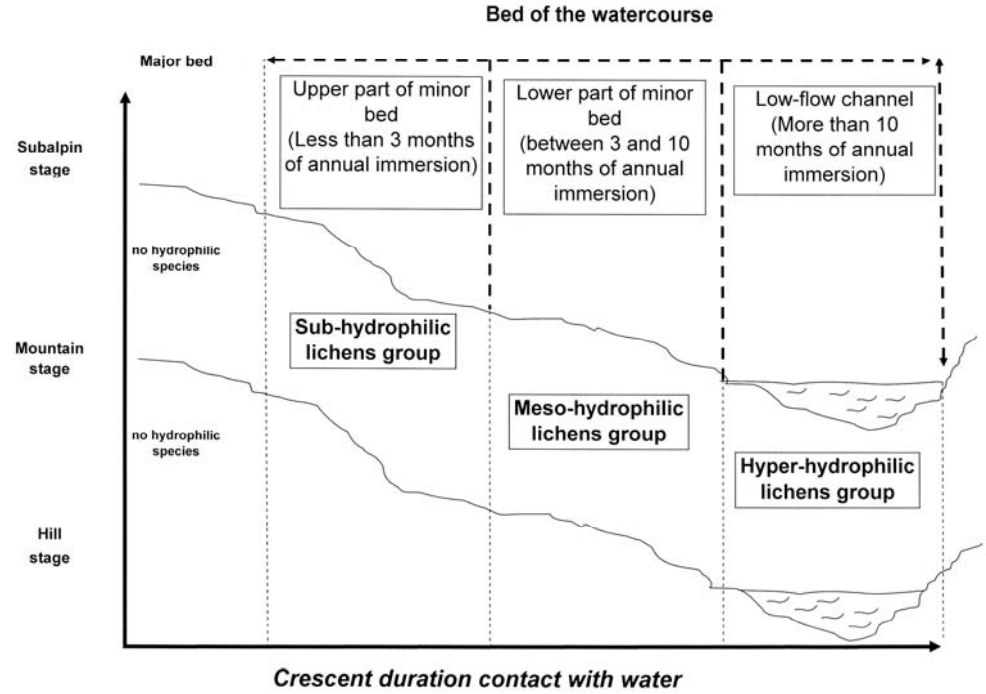

Fig. 6 : Ecological description of lichen groups on the banks of watercourses.