Notes on the herbivory on *Buxbaumia viridis* sporophytes in the Pyrenees

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**Abstract** – *Buxbaumia viridis* is a bryophyte whose gametophyte is highly reduced, while its sporophyte is relatively large, present all year round in its different phenological stages. In the Pyrenees, where the species is present in humid forests, especially pure *Abies alba* or mixed *A. alba* and *Fagus sylvatica* forests, the sporophytes mature in spring, losing their winter green colour. Herbivory has been detected on young capsules in spring. Observed damages are mainly of two types: cut setae, where capsule is completely lost and whose responsible organism has not been identified; and more frequently, torn capsules where sporal mass is partly gone, sometimes only part of the theca at the base of the capsule remains. The responsible organisms in the second type are young slugs (genus *Arion*), what have been observed *in situ* twice. The animal tears the capsule and scrapes with its radula the sporal mass from the inside. Between 1999 and 2014, we visited 40 localities with *Buxbaumia viridis* populations, located in Navarra and Huesca on the southern versant of the Pyrenees, and Pyrénées-Atlantiques and Hautes-Pyrénées on the northern versant, aiming to estimate the number of individuals. Grazing on *B. viridis* capsules has been detected in 28 of these localities (70%), proving that this consumption is not accidental. Regarding the grazing rate, 10 localities showed consumption less than 20% of the total sporophyte number, 14 a consumption ranging from 21 to 59%, and finally, 4 were over 60% of grazed sporophytes. This sporophyte consumption is so high that it might have an important incidence on the species conservation.

**Mosses / Europe / Spain / France / slugs / grazing**

**INTRODUCTION**

Traditionally, the consumption of bryophytes by animals has been considered a rare case and not important from a quantitative point of view. Nevertheless, feeding on bryophytes has been accepted for different animal groups, including bears, some micromammals, slugs and several insect groups (Orthoptera, Coleoptera, moths, aphids, flies and ants). Gerson (1982) and Glime (2017) present a general perspective on bryophyte consumption. Regarding specifically *Buxbaumia viridis* in the Pyrenees, grazing on its sporophytes had been previously detected in 1999 (Infante & Heras, 2001).

*Buxbaumia viridis* (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl. has a gametophyte reduced to chlorophyllic filaments, which are not perceptible in the

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field. Its sporophyte is, on the contrary, rather large (1-1.8 cm) and visible all year round in its different phenological stages. In the Pyrenees, fertilization happens from mid spring to early summer; young sporophytes begin being perceptible by late summer and early fall. At this stage their capsules are green and more or less cylindrical, and remain so for the winter. In early spring, capsules begin to mature, developing their particular shape and acquiring gradually a brownish colour. Finally, in late spring and early to mid summer, its dorsal cuticle tears apart, the operculum falls off and the spore dispersal is possible. Dry and empty capsules may remain even until the next season.

In the Pyrenees, *Buxbaumia viridis* is a preferentially lignicolous species living on dead wood in humid forests. Three forest types have been recognized as its potential habitat: pure *Abies alba* Mill. and mixed *A. alba* and *Fagus sylvatica* L. forests, which are the most relevant for the species; and to a lesser extent, *Pinus uncinata* Ramond ex DC. in Lam. & DC. or *P. sylvestris* L. pinewoods. The moss colonizes mainly permanently humid dead conifer wood, although it also has been detected rarely on beech wood. Following the Söderström decomposition scale (Söderström, 1988), colonized decomposition stages range from 4 to 8, but most individuals have been observed on wood in stages 5 to 7.

*Buxbaumia viridis* is a boreal montane circumpolar species, present in Europe from southern Scandinavia to southern mountain ranges (Pyrenees, Alps, Carpathians, and Corsican Mountains). Its distribution area is in fact rather large, but its population density is low (Infante & Heras, 2001; Table 1), and its ability to occupy favourable substrates seems rather limited (Wiklund, 2002).

It is listed in Annex II of the European Union Council Directive 92/43/EEC (Habitats Directive), and this has caused an unprecedented attention for this bryophyte. Observations have multiplied since 1992. In Spain, *B. viridis* is considered as “Vulnerable” by criteria B2ab(ii, iii, iv) (Brugués et al., 2014); in the French Midi-Pyrénées region, it is considered as “Near Threatened” by criteria pr. B2b(iii) (Infante Sánchez et al., 2015). In both territories, the main threat for this species is the intense forest exploitation. This reduces the dead wood pieces that constitute the preferential habitat of *B. viridis*.

Recent modelling made for Sweden resulted in negative predictions for *B. viridis* survival in the long term under different climate change scenarios (Ruete et al., 2012), and in Switzerland, the analysis of herbarium data show how the species has been regressing for the last two centuries (Hofman et al., 2007).

**MATERIAL AND METHODS**

In the context of the monitoring of *Buxbaumia viridis* for compliance with Habitats Directive, from both northern and southern slopes in the Pyrenees, efforts have been made to complete knowledge on the species distribution (Fig. 1), its local ecology and populations. Although no global Pyrenean project has been attempted, monitoring in the central-western Pyrenees has converged over the years in a similar methodology. So, between 1999 and 2014, 40 localities with *Buxbaumia viridis* populations, located in Navarra and Huesca (Spanish and southern versant of the Pyrenees), and Pyrénées-Atlantiques and Hautes-Pyrénées (French and northern Pyrenean versant), have been visited, aiming to estimate the number of individuals.
Table 1. Localities of *Buxbaumia viridis* visited between 1999 and 2014. Country, ESP = Spain, FR = France; department, HU = Huesca, NA = Navarra, HP = Hautes-Pyrénées, PA = Pyrénées-Atlantiques

<table>
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<tr>
<th>Country, Department:</th>
<th>Year</th>
<th>Area m²</th>
<th>Dead wood pieces colonized by <em>Buxbaumia viridis</em></th>
<th>Density (Dead wood pieces colonized by <em>Buxbaumia viridis</em> /1000 m²)</th>
<th>Number of <em>Buxbaumia viridis</em> sporophytes</th>
<th>Number of grazed <em>Buxbaumia viridis</em> sporophytes</th>
<th>Percentage of grazed <em>Buxbaumia viridis</em> sporophytes</th>
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The methodology for the counting of *Buxbaumia viridis* individuals in Habitats Directive considers each piece (fallen trunks and stumps) of colonized dead wood as a single individual. On each of the visited localities, within a variable area, the number of dead wood pieces colonized by *B. viridis* (equals number of individuals *sensu* Habitats Directive), total number of detected *B. viridis* sporophytes and number of grazed *B. viridis* sporophytes were noted. For some of the localities visited in 1999, only area, number of occupied pieces and percentage of grazed sporophytes are still available (Table 1).

**RESULTS**

During the monitoring of the different localities, different types of anomalies or damages were observed on *Buxbaumia viridis* sporophytes. Some were obviously fungal development leading to capsule abortion, but two other damage types, ascribable to herbivory, were much more frequent:

– damage type 1, cut setae (Fig. 2). In this case, there is no trace left of the capsule and it must be stressed how the cut is usually very neat, so the possibility of accidental fall or break was soon discarded. The cut setae showed the same colour and turgidity as the setae of entire sporophytes around them, so with some experience, it was not difficult to tell apart the remains of an old sporophyte from last season from these cut setae. The grazer or, most probably, several grazers, in this case, have not yet been identified.

– damage type 2, torn capsules. In this case, the theca may partially remain, although more or less empty, and often the bases bearing rests of the sporal mass can be seen (Figs 3, 4). Twice, young slugs were observed while feeding on *Buxbaumia viridis* young capsules (Figs 5, 6), leaving this kind of damage behind. This damage type was attributed to these invertebrates.
Herbivory on *Buxbaumia viridis* in the Pyrenees

Fig. 2. Damage type 1: cut seta to the left. Photo: P. Heras.

Fig. 3. Damage type 2, torn capsule with scraped off sporal mass. Photo: P. Heras.
Fig. 4. Damage type 2, torn capsule with base still showing sporal mass. Photo: P. Heras.

Fig. 5. Slug feeding on *Buxbaumia viridis*, Navarra, after forcing it to show ventral side. Photo: P. Heras.
In both cases, observed grazing slugs fell into juvenile individuals in the genus *Arion* Férussac 1819. These animals use their radula to incise the exothecium and scrape the sporal mass. They find their food by their olfactory organs, and in optimal conditions, they can travel foraging from 2 to 7 metres a day.

Glime (2017: 19) has pointed out that apparent herbivory on the capsules of a close species, *Buxbaumia aphylla* Hedw., is really just the capsule splitting by the sides after drying, uncovering sporal mass. This kind of damage has not been observed. In contrast to *B. aphylla*, *B. viridis* rarely dries out, because of its habitat conditions; and it lacks a neat lateral side that could allow this splitting, as that of *B. aphylla*.

Feeding has only been observed in late spring (early summer), while capsules are not yet completely mature, the cuticle is just about to begin tearing to the sides of the capsule and the opercula are still in place. The process stops in the summer and fall.

In the counting of sporophytes, just the total number of missing or damaged capsules was noted, without differentiating the losses by the different types. Table 1 shows a compilation for all 40 localities investigated over the time (1999-2014).
Herbivory on *Buxbaumia viridis* sporophytes has been detected in 70% of the studied localities all over the central-western Pyrenees (Fig. 7). The localities where herbivory was not detected, usually only contained 1-2 (3) colonized dead wood pieces with a very small total number of sporophytes (1-3(8)), probably hindering their finding by grazers.

The average consumption percentage of the sporophyte total number in the Pyrenees is 30%, but 10% of the localities show very high consumption rates over 60%. In Scotland, high consumption rates on *Buxbaumia viridis* sporophytes (62-89%) have also been recorded (Rothero, 2008); slugs, snails, birds and small mammals were pointed as potential culprits.

As grazing by slugs has been proved in the Pyrenees, it should be noted how slugs and *Buxbaumia viridis* share some common traits in their life cycles: both have their fertilization process in late spring and early summer, and their populations may be limited by lack of humid conditions in that season; slugs hatch in late summer and early fall, at the same time that *B. viridis* sporophytes begin to be perceptible; very dry and cold winters complicate their survival; whereas temperature rising in spring triggers the final maturation of *B. viridis* sporophytes and the exit of hungry young slugs from their winter refuges.

Regarding grazing candidates for damage type 1, it must be noted that the fauna is rather limited in high altitude Pyrenean forests. For example, ants are common and numerous inhabitants of these woods; in particular *Formica rufa* Linnaeus 1761, responsible for the big dome-shaped nests that can be easily seen. Although they are omnivorous, a great deal of their diet is actually other insects, so grazing on *Buxbaumia viridis* would only be occasional, although not discardable. Small mammals, as for instance, *Apodemus sylvaticus* Linnaeus 1758 (wood mice),
primarily seed eaters and residents in these conifer woods, are another possibility, as well as birds like *Lophophanes cristatus* Linnaeus 1758 (crested tit), or *Periparus ater* Linnaeus 1758 (coal tit), both small birds (10-13 cm), also resident in these woods, nesting not far from forest floor, and feeding on insects and seeds to whom a 0.5 cm capsule could be attractive. The presence of bryophyte sporophytes in the diets for these animals should be further investigated.

As for the consequences of this grazing, it has already been suggested that sporophyte consumption by animals, particularly by slugs, could actually be a vector of bryophyte dispersion, since transit through the digestive tract might not destroy completely the sporophyte (Davidson *et al.*, 1990). Müller (2012) also points out that openings made on the sporophytes of a close species, *Buxbaumia aphylla*, by snails and/or slugs, allow the consumption of the sporal mass by flies (Mycetophilidae), attributing to these last animals a bryophyte dispersing potential.

In the Pyrenees, feeding on *Buxbaumia viridis* is made only on young sporophytes, before complete spore maturation and dehiscence of the capsule. A similar pattern has already been observed by Estébanez *et al.* (2005), who have recorded feeding by slugs only on young capsules of several *Grimmia* species. These authors, examining starch, sugar and lipidic content in *Grimmia pulvinata* sporophytes through all their phenological stages, have shown how young capsules barely contained any lipids in contrast to more mature capsules, while starch and sugar content showed their maximum in younger capsules, although high levels also were detected in subsequent stages. Lipidic content is maximal just before the expansion of the maturing capsule and this could point to a protective role against herbivores, a topic that should be further investigated.

Since feeding occurs before complete spore maturation and dehiscence of the capsule, it is hard to believe that grazing could be beneficial for *Buxbaumia viridis*. Then the loss of an important part of the sporophytes produced each year might have a serious impact on *Buxbaumia viridis* populations.

Taking into account that *Buxbaumia viridis* is considered a fugitive species (Dierssen, 2001) dependent on a substrate type, the decaying wood, in rapid turnover, grazing impact might be even worse. It could be assumed that in natural conditions, with an adequate dead wood dynamics, *B. viridis* should be able to survive its grazers. However, in harvested forests where most or all the dead wood is removed, the number of individuals of *B. viridis* is highly reduced; grazing on the few sporophytes produced in these cases could be fatal. As grazing could be an important factor to be considered in the conservation and management of this catalogued species, it is also worth pointing out how effective solutions might not be easy to find.

CONCLUSIONS

Herbivory on *Buxbaumia viridis* sporophytes is not an isolated phenomenon, but geographically spread in the Pyrenees. Several grazers seem to be involved given the different types of damage observed, but so far only slugs have been confirmed.

Grazing is quantitatively important, since average loss of sporophytes in the Pyrenees is 30%. Most important is that capsules are consumed in an early stage, before maturation of spores, so grazing should be interpreted in a negative way for
B. viridis, in particular in areas where forest exploitation reduces the available substrate and alters its natural dynamics, eventually complicating the species survival in the long term.

As a catalogued species at the European level, listed in Annex II of Habitats Directive, grazing should be taken into account in eventual management plans.

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